Putting keyhole limpets on the map: phylogeny and biogeography of the globally distributed marine family Fissurellidae (Vetigastropoda, Mollusca)

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ABSTRACT

Fissurellidae are marine gastropods with a worldwide distribution and a rich fossil record. We integrate molecular, geographical and fossil data to reconstruct the fissurellid phylogeny, estimate divergence times and investigate historical routes of oceanic dispersal. With five molecular markers for 143 terminals representing 27 genera, we resolve deep nodes and find that many genera (e.g., *Emarginula*, *Diodora*, *Fissurella*) are not monophyletic and need systematic revision. Several genera classified as Emarginulinae are recovered in Zeidorinae. Future work should prioritize emarginuline genera to improve understanding of ancestral traits and the early evolution of fissurellids. Tree calibration with the fossilized birth-death model indicates that crown fissurellids originated around 175 Ma, and generally resulted in younger ages for the earliest nodes than the node dating approach. Model-based biogeographic reconstruction, supported by fossils, infers an Indo-West Pacific origin, with a westward colonization of new oceans via the Tethys Seaway upon the breakup of Pangea. Western Atlantic clades then served as source for dispersal towards other parts of the globe. As the sister group to all other fissurellids, *Rimula* is ranked in its own subfamily, Rimulinae **stat. nov.** New synonyms: Hemitominae **syn. nov.** of Zeidorinae **stat. nov.**; *Cranopsis* **syn. nov.** of *Puncturella*; *Variegemarginula* **syn. nov.** of *Montfortula*.

1. Introduction

As the oldest and some of the most diverse groups of animals on the planet, marine invertebrates have great potential for expanding our knowledge about the historical forces shaping biodiversity. With more than 500 extant species in 48 genera (WoRMS, 2018), a worldwide distribution and a fossil record tracing back to the mid-Phanerozoic, the family Fissurellidae J. Fleming, 1822 can provide insights about the origins and maintenance of marine biodiversity and about historical routes of oceanic dispersal. Yet, essential information including a robust phylogeny of the family and the time of diversification are still lacking.

Fissurellids live on rocky substrates, from the intertidal down to depths of thousands of meters. A characteristic feature of their limpet-shaped shell is the presence of a foramen through which water with waste is disposed from the mantle cavity and through which gametes are released. Shells with similar foramina are also characteristic of

other vetigastropods, such as abalones, slit shells, little slit shells, and many gastropod fossils (Geiger et al., 2008). It is not clear however how many times such respiratory foramina have appeared or been lost in Vetigastropoda Salvini-Plawen, 1980. In fissurellids, a wide variation exists in the shape of the shell and in the shape and position of the foramen: shells range from flat to conical with either an anterior marginal notch or slit, an apical or subapical foramen, or an imperforate shell. The factors that might have led to such a diversity of patterns, or their implications for the physiology and evolution of the animals are unclear, but it has been suggested that secondarily imperforate shells could represent an adaptation to harsh intertidal habitats (Aktipis et al., 2011). Features of the shell and the radula have played an important role in the taxonomy and classification of the family (Bouchet et al., 2017; Knight et al., 1960; Thiele, 1929), which has had from two to six accepted subfamilies along its history (see Aktipis et al. 2011 for a thorough historical review of classifications). Understanding the

evolution and transitions between shell forms, however, requires an adequately sampled and well resolved phylogeny.

The first morphological cladistic analysis of fissurellids (McLean and Geiger, 1998) included what were then members of the subfamily Emarginulinae Children, 1834. The branching order of the different genera indicated the progressive evolution of the position of the shell foramen, with the marginal slit characteristic of *Emarginula* Lamarck, 1801 considered the plesiomorphic condition and the apical foramen the derived condition. However, due to its early presence in the fossil record, the genus *Emarginula* was fixed as the outgroup (McLean and Geiger, 1998), preventing the estimation of the position of *Emarginula* in the tree and confusing the proper tracing of the evolutionary history of the foramen.

The most significant molecular insight into fissurellid systematics to date was a five-gene phylogeny (Aktipis et al., 2011), in which some genera traditionally considered part of Emarginulinae were recovered as a separate group and reinstated as the subfamily Hemitominae Kuroda, Habe & Oyama, 1971. The position of Hemitominae as the sister group to all other fissurellids contradicted the hypothesis of the straightforward progression of the shell foramen because its members present non-perforated shells or shells with a subapical foramen. In the same year, these molecular results were questioned, and the subfamily Hemitominae was reinstated with a contrasting generic composition based on shell and radular characters, but without a phylogenetic framework (McLean, 2011). Because of the unexpected rearrangement in the molecular phylogeny, and because taxonomic sampling was a small fraction of the known diversity, further data remained necessary to resolve the phylogeny of Fissurellidae.

The family has a global distribution and is assumed to date back to the Triassic (Geiger et al., 2008), when the current landmasses coalesced forming the supercontinent Pangea. Given their long history, it is hard to track how fissurellids spread to colonize the modern oceans, especially without knowing their center of origin and pattern of diversification. Discrete barriers are hard to recognize in the marine realm, and larval dispersal has been considered an important mechanism in maintaining wide connectivity and large ranges in the distribution of marine species (e.g., Scheltema and Williams, 1983; Scheltema, 1971). Although exceptions exist, planktotrophic larvae are expected to spend longer periods in the plankton, and therefore reach wider ranges than non-feeding larvae (Jablonski and Lutz, 1983; McEdward, 1995; Selkoe and Toonen, 2011). Nonetheless, strong genetic structure has been shown not only for species with short-lived larvae or direct development, but also for marine invertebrates with long-lived planktonic larvae (Kawauchi and Giribet, 2014; Kelly and Palumbi, 2010). Fissurellids are members of the Vetigastropoda, a group of mostly broadcast spawners with short-lived, non-feeding larvae (Giese and Pearse, 1977; Hadfield et al., 1997; Strathmann, 1978; Young, 2002). Scattered studies on fissurellid reproduction and early development show very short larval spans of only a few days (Lewis, 1960; Reynoso-Granados et al., 2007) or non-planktonic development (Pernet, 1997), in line with studies showing strong genetic structure at small geographical scales (R.L. Cunha et al., 2017; Waters et al., 2007).

Although the family has a worldwide distribution, evidence for limited capacity for dispersal leads to the hypothesis that diversity within the family should have a structured geographical distribution. Furthermore, a better understanding of the phylogeny, in combination with geographical data from modern and fossil fissurellids, could provide insights about the main routes of dispersal of marine organisms upon the separation of landmasses and formation of new oceans during the Mesozoic era. Given that gastropods in general had a broad distribution around the continental margins of Pangea in the late Paleozoic and early Mesozoic (Paleobiology Database, 2019), we aim to pinpoint the center of origin of the family, and to evaluate the most likely routes of marine dispersal as new oceans opened.

Using a five-gene phylogeny, we greatly expand taxon sampling to elucidate deep relationships between subfamilies and the placement of a broader diversity of genera. We then present time-calibrated trees based on dozens of fossil ages with two distinct methods, and use model-based biogeographical analyses to estimate ancestral ranges and discuss the colonization of the world's oceans by fissurellids.

2. Methods

2.1. Taxon sampling

We present the largest taxon sampling of fissurellids by sequencing 127 individuals and analyzing them in conjunction with 16 other species for which sequences were publicly available in the GenBank database (Table 1). The new specimens come from large-scale expeditions and research cruises, as well as smaller scale collections by the authors, and are complemented by a few older museum specimens. In total, there are 143 ingroup taxa from 27 genera that reflect the worldwide distribution of fissurellids (Fig. 1) and correspond to twice as many genera compared to a previous molecular phylogeny (Aktipis et al., 2011). One Cocculiniformia and nine other vetigastropods were included as outgroups. Specimens were preserved in 96% ethanol and are deposited in the following institutions: Muséum National d'Histoire Naturelle (MNHN), Museum of Comparative Zoology (MCZ), Museu de Zoologia da Universidade de São Paulo (MZSP), KwaZulu-Natal Museum (NMP), and Atmosphere and Ocean Research Institute, The University of Tokyo (AORI). See Table 1 for voucher numbers, GenBank accession codes and specimen information.

2.2. Molecular methods

Sequence data for five molecular markers were acquired with PCR and Sanger sequencing. Total DNA was extracted from foot or mantle tissue using the DNeasy tissue kit (Qiagen), and used as PCR templates for the amplification of the ribosomal nuclear genes 18S and 28S rRNA, the nuclear protein-coding histone H3, and the mitochondrial 16S rRNA and cytochrome *c* oxidase subunit I (COI). Due to their length, the nearly complete 18S rRNA and ca. 2 Kb of the 28S rRNA were each sequenced with three mostly overlapping fragments; primer sequences are listed in Table 2. Amplification was performed in 25 µl reactions consisting of 1 µl of template DNA, 0.25 µl of each primer (100 nM), 0.5 µl of dNTPs (100 nM), 5 µl of 5x PCR buffer, 0.13 µl of GoTaq DNA polymerase (Promega) and molecular grade deionized water up to 25 µl. Bovine serum albumin (BSA) was included replacing 2 µl of water to optimize some reactions. Amplification conditions were: initial denaturing at 95 °C for 2 min, followed by 35 cycles of 30 s at 95 °C, 30 s at 47/54 °C (Table 2) and 3 min at 72 °C, and final extension at 72 °C for 5 min. PCR products were visualized on 1% agarose gels and purified using ExoSAP-IT (Affymetrix). Sequencing reactions used Big-Dye Terminator 3.1 (Applied Biosystems); products were purified with Sephadex (Amersham Biosciences) and sequenced on an ABI Prism 3730 Genetic Analyzer (Applied Biosystems). Sequences were assembled and edited in Geneious Pro 9.1.7 (Kearse et al., 2012) and Sequencher 5.1 (Gene Codes Corporation). Sequences were screened for contamination using BLAST searches and maximum likelihood gene trees. New sequences are deposited in GenBank (Table 1).

2.3. Phylogenetic analyses

We used Bayesian inference and maximum likelihood to reconstruct the fissurellid phylogeny from an aligned and concatenated dataset of 7138 bp. Sequences of each gene fragment were first aligned using MAFFT 7.222 (Katoh and Standley, 2013), implemented in Geneious; the L-INS-i alignment algorithm was used for the ribosomal genes, and the G-INS-i algorithm for the protein coding genes. For 18S rRNA and 28S rRNA, for which we sequenced three fragments each, the overlapping ends were trimmed before concatenation. The five genes were

Table 1

Voucher information and GenBank accession numbers for specimens used in the molecular analyses. New sequences are in bold. New synonyms are marked with an asterisk (*Variegemarginula* **syn. nov.** of *Montfortula*; *Cranopsis* **syn. nov.** of *Puncturella*). Repositories: MCZ, Museum of Comparative Zoology; MNHN, Muséum National d'Histoire Naturelle; MZSP, Museu de Zoologia da Universidade de São Paulo; KwaZulu-Natal Museum (NMP); AORI, Atmosphere and Ocean Research Institute, The University of Tokyo. More specimen information can be found at the voucher links and the Supplementary Material.

Species	Voucher	Country	18Sa rRNA	18Sb rRNA	18Sc rRNA	28Sa rRNA	28Sb rRNA	28Sc rRNA	H3	16S rRNA	COI
Diodorinae											
Cosmetalepas concatenata	MNHN 2009 14162	Madagascar	MK322218	MK322218	MK322218	MK331071	MK331645	MK331645	MK291192	MK322130	MK291039
Diodora aspera	MCZ 377783	USA	MK322176	MK322176	MK322176	MK331028	MK331609	MK331609	MK291176	MK322096	–
Diodora cayenensis	MCZ 378366	Bahamas	MK322180	MK322180	MK322180	–	MK331611	MK331611	MK291147	MK322067	MK291019
Diodora cayenensis	MZSP 103772	Brazil	MK322246	MK322246	MK322246	MK331001	MK331122	–	MK291148	MK322071	MK291017
Diodora cayenensis	MCZ 378371	Panama	MK322181	MK322181	MK322181	MK330999	MK331612	MK331612	MK291168	MK322070	MK291015
Diodora cayenensis	MCZ 378372	USA	MK322182	MK322182	MK322182	MK331000	MK331613	MK331613	MK291150	MK322073	MK291012
Diodora cayenensis	MCZ 378375	USA	MK322183	MK322183	MK322183	MK331019	MK331614	MK331614	MK291152	MK322074	MK291013
Diodora cf. cruciata	MNHN 2013 14812	Papua New Guinea	MK322227	MK322227	MK322227	MK331005	MK331658	MK331658	MK291160	MK322088	MK291026
Diodora cf. quadrirradiatus	AORI_YK2601	Thailand	MK322160	MK322160	MK322160	MK331014	MK331595	MK331595	MK291165	MK322089	MK291030
Diodora cf. saturnalis	MCZ 378397	USA	MK322186	MK322186	MK322186	MK331029	MK331617	MK331617	–	–	MK291031
Diodora cf. sieboldi	AORI_YK2598	Japan	MK322158	MK322158	MK322158	MK331008	MK331593	MK331593	MK291162	MK322087	MK291029
Diodora crucifera	MCZ 378406	South Africa	MK322189	MK322189	MK322189	MK331013	MK331620	MK331620	–	MK322090	MK291033
Diodora galeata	MNHN 2013 15214	Papua New Guinea	MK322229	MK322229	MK322229	MK331011	MK331660	MK331660	MK291156	MK322094	MK291033
Diodora galeata	MNHN 2013 3769	Papua New Guinea	MK322238	MK322238	MK322238	MK331012	–	MK331127	MK291157	MK322095	MK291034
Diodora gibberula	MCZ 378378	Spain	GQ160789	GQ160789	GQ160789	GQ160637	GQ160637	GQ160637	GQ160723	GQ160684	GQ160752
Diodora gibberula	MCZ 378383	Spain	MK322184	MK322184	MK322184	MK331017	MK331615	MK331615	MK291164	MK322066	MK291038
Diodora graeca	MNHN 2009 5224	Spain	MK322225	MK322225	MK322225	MK331027	MK331654	MK331654	MK291153	MK322092	MK291080
Diodora kraussi	MCZ 378391	South Africa	MK322185	MK322185	MK322185	MK331010	MK331616	MK331616	MK291154	–	–
Diodora lineata	MCZ 378393	Australia	HM771456	HM771456	HM771456	HM771502	HM771502	HM771502	HM771584	HM771542	HM771621
Diodora listeri	MCZ 378395	Bermuda	HM771450	HM771450	HM771450	HM771495	HM771495	HM771495	HM771578	HM771538	HM771616
Diodora mus	AORI_YK2599	Japan	MK322159	MK322159	MK322159	MK331015	MK331594	MK331594	MK291159	MK322082	MK291024
Diodora quadrirradiatus	AORI_YK2602	Japan	MK322161	MK322161	MK322161	MK331006	MK331596	MK331596	MK291166	MK322093	MK291025
Diodora sieboldi	AORI_YK2597	Japan	MK322157	MK322157	MK322157	MK331022	MK331592	MK331592	MK291163	MK322084	MK291032
Diodora singaporensis	MCZ 378398	Australia	HM771458	HM771458	HM771458	HM771504	HM771504	HM771504	HM771586	HM771544	HM771623
Diodora sp.	MZSP 115673	Brazil	MK322252	MK322252	MK322252	MK331003	MK331676	MK331676	–	–	–
Diodora sp.	MZSP 104559	Brazil	MK322248	MK322248	MK322248	MK331002	MK331121	–	MK291149	MK322072	MK291018
Diodora sp.	MCZ 378404	China	MK322188	MK322188	MK322188	MK331021	MK331619	MK331619	MK291155	MK322083	MK291028
Diodora sp.	MCZ 392709	India	MK322149	MK322149	MK322149	MK331020	MK331586	MK331586	MK291175	MK322080	MK291027
Diodora sp.	MCZ 383321	Panama	MK322211	MK322211	MK322211	MK330998	MK331639	MK331639	MK291173	MK322069	MK291014
Diodora sp.	MCZ 378403	USA	MK322187	MK322187	MK322187	MK331018	MK331618	MK331618	MK291151	MK322068	MK291016
Diodora sp.1	MNHN 2013 5629	Papua New Guinea	MK322239	MK322239	MK322239	MK331023	MK331665	MK331665	MK291158	MK322081	–
Diodora sp.10	MNHN 2009 25065	Mozambique	MK322221	MK322221	MK322221	–	MK331649	MK331649	–	MK322091	–
Diodora sp.2	MNHN 2013 18331	Papua New Guinea	MK322234	MK322234	MK322234	MK331007	MK331662	MK331662	MK291161	MK322086	–
Diodora sp.2	MNHN 2013 17999	Papua New Guinea	MK322232	MK322232	MK322232	MK331009	MK331118	–	–	MK322085	–
Diodora ticaonica	MCZ 378401	Australia	HM771457	HM771457	HM771457	HM771503	HM771503	HM771503	HM771585	HM771543	HM771622
Fissurellidea megatrema	MZSP 110103	Brazil	MK331695	MK331695	–	–	MK331103	MK331103	MK291178	–	–
Lucapina aegis	MCZ 381345	Panama	MK322209	MK322209	MK322209	–	MK331638	MK331638	MK291169	MK322077	MK291037
Lucapina aegis	MCZ 376771	Panama	MK322175	MK322175	MK322175	MK331004	MK331608	MK331608	MK291167	MK322075	MK291035
Lucapina sowerbii	MZSP 104588	Brazil	MK331681	MK331681	–	MK331016	MK331674	MK331674	MK291170	MK322078	MK291023
Lucapina sowerbii	MCZ 378569	USA	MK322197	MK322197	MK322197	MK331025	MK331626	MK331626	MK291171	–	MK291021
Lucapina sowerbii	MCZ 378573	USA	MK322199	MK322199	MK322199	MK331026	MK331627	MK331627	MK291172	–	MK291022
Lucapina sp.	MCZ 378574	Panama	MK322200	MK322200	MK322200	MK331024	MK331628	MK331628	MK291128	MK322076	MK291036
Lucapina suffusa	MCZ 378571	Panama	MK322198	MK322198	MK322198	–	MK331110	–	MK291174	MK322079	MK291020
Megathura crenulata	MCZ 378581	USA	HM771459	HM771459	HM771459	HM771505	HM771505	HM771505	HM771587	MK322097	–
Monodilepas monilifera	MCZ 381310	New Zealand	MK331677	MK331677	–	MK331030	MK331635	MK331635	MK291177	–	MK291040

Table 1 (continued)

Species	Voucher	Country	18Sa rRNA	18Sb rRNA	18Sc rRNA	28Sa rRNA	28Sb rRNA	28Sc rRNA	H3	16S rRNA	COI
Emarginulinae											
Emarginula cf. huzardii	MCZ 392707	India	MK322147	MK322147	MK322147	MK331075	MK331584	MK331584	MK291099	MK322134	–
Emarginula concinna	AORI_YK2607	Japan	MK322163	MK322163	MK322163	–	MK331598	MK331598	MK291086	MK322132	MK291048
Emarginula eximia	AORI_YK2614	Japan	MK322166	MK322166	MK322166	MK331064	MK331601	MK331601	MK291179	MK322133	MK291049
Emarginula maculata	AORI_YK2623	Philippines	MK322171	MK322171	MK322171	MK331074	MK331604	MK331604	MK291102	MK322137	MK291066
Emarginula octaviana	MCZ 376614	Spain	MK322172	MK322172	MK322172	MK331061	MK331605	MK331605	MK291083	–	–
Emarginula sicula	MCZ 376615	Spain	MK322173	MK322173	MK322173	MK331060	MK331606	MK331606	MK291084	–	MK291047
Emarginula sp.	MCZ 378422	Panama	MK322191	MK322191	MK322191	MK331059	MK331621	MK331621	MK291188	MK322140	MK291069
Emarginula sp.12	MNHN 2013 6070	Papua New Guinea	MK322243	MK322243	MK322243	MK331063	MK331670	MK331670	MK291085	MK322131	MK291046
Emarginula sp.2	MNHN 2007 34749	New Caledonia	MK322215	MK322215	MK322215	MK331078	–	MK331126	MK291097	MK322138	–
Emarginula sp.3	MNHN 2007 31432	Philippines	MK322213	MK322213	MK322213	MK331073	MK331641	MK331641	MK291096	MK322136	MK291065
Emarginula sp.6	MNHN 2013 11875	Papua New Guinea	MK322226	MK322226	MK322226	MK331062	MK331656	MK331656	–	–	–
Emarginula sp.7	MNHN 2013 6333	Papua New Guinea	MK322244	MK322244	MK322244	MK331072	MK331671	MK331671	MK291101	MK322135	MK291064
Emarginula sp.A	MNHN 2013 18121	Papua New Guinea	MK331678	MK331678	–	–	–	MK331124	MK291100	MK322141	MK291068
Emarginula sp.B	MNHN 2013 16712	Papua New Guinea	MK331696	–	–	MK331076	–	–	MK291120	MK322129	MK291070
Montfortula brevirimata	MNHN 2009 14033	Madagascar	MK322217	MK322217	MK322217	–	MK331644	MK331644	MK291185	MK322125	MK291051
Montfortula chathamensis	MCZ 381311	New Zealand	MK322207	MK322207	MK322207	MK331067	MK331636	MK331636	MK291181	MK322128	MK291053
Montfortula picta	AORI_YK2609	Japan	MK322164	MK322164	MK322164	MK331066	MK331599	MK331599	MK291184	MK322124	MK291042
Montfortula punctata *	AORI_YK2605	Japan	MK322162	MK322162	MK322162	MK331070	MK331597	MK331597	MK291189	–	–
Montfortula rugosa	MCZ 378592	Australia	HM771435	HM771435	HM771435	HM771480	HM771480	–	HM771563	HM771524	HM771607
Montfortula sp.1	MNHN 2013 15194	Papua New Guinea	MK322228	MK322228	MK322228	MK331065	MK331659	MK331659	MK291183	MK322127	MK291052
Montfortula sp.2	MNHN 2013 57670	Tasmania	MK322241	MK322241	MK322241	MK331068	MK331667	MK331667	MK291182	MK322126	MK291041
Montfortula variegata *	AORI_YK2615	Japan	MK322167	MK322167	MK322167	MK331069	MK331115	–	MK291180	MK322123	MK291067
Scelidotoma gigas	AORI_YK2620	Japan	MK322170	MK322170	MK322170	MK331077	MK331603	MK331603	MK291098	MK322139	MK291067
Scutus antipodes	MCZ 378726	Australia	HM771438	HM771438	HM771438	HM771483	HM771483	–	HM771566	HM771527	HM771608
Scutus breviculus	AORI_YK196	New Zealand	MK322151	MK322151	MK322151	MK331058	MK331588	MK331588	MK291090	MK322115	AB365215
Scutus forsythi	MCZ 378598	Australia	HM771443	HM771443	HM771443	HM771488	HM771488	HM771488	HM771571	HM771531	HM771611
Scutus howensis	MCZ 378728	Australia	HM771441	HM771441	HM771441	HM771486	HM771486	HM771486	HM771569	HM771529	–
Scutus sinensis	MCZ 378729	China	MK322202	MK322202	MK322202	MK331052	MK331630	MK331630	MK291089	MK322118	MK291044
Scutus sp.	MCZ 392708	India	MK322148	MK322148	MK322148	MK331050	MK331585	MK331585	MK291087	MK322116	MK291043
Scutus unguis	MCZ 378730	Australia	MK322203	MK322203	MK322203	MK331053	MK331631	MK331631	–	MK322119	MK291054
Scutus unguis	MNHN 2013 14776	Papua New Guinea	MK331689	–	MK331700	MK331051	MK331657	MK331657	MK291088	MK322117	–
Tugali cicatricosa	MNHN 2013 57685	Tasmania	MK331680	MK331680	–	MK331056	MK331669	MK331669	MK291092	MK322121	MK291045
Tugali decussata	AORI_YK2610	Japan	MK322165	MK322165	MK322165	MK331057	MK331600	MK331600	MK291093	MK322122	–
Tugali elegans	MCZ 381306	New Zealand	MK322206	MK322206	MK322206	–	MK331634	MK331634	MK291094	MK322120	MK291050
Tugali parmophoidea	MCZ 378776	Australia	MK322204	MK322204	MK322204	MK331055	MK331632	MK331632	MK291091	–	–
Tugali suteri	MCZ 381312	New Zealand	MK322208	MK322208	MK322208	MK331054	MK331637	MK331637	MK291095	–	–
Fissurellinae											
Amblychilepas javanicensis	MNHN 2013 57675	Tasmania	MK331679	MK331679	–	MK331039	MK331668	MK331668	MK291130	MK322102	MK291059
Amblychilepas nigrita	MCZ 378229	Australia	HM771471	HM771471	HM771471	HM771517	HM771517	HM771517	HM771599	MK322101	MK291058
Amblychilepas oblonga	MNHN 2013 18068	Papua New Guinea	MK322233	MK322233	MK322233	MK331048	MK331661	MK331661	MK291145	–	–
Amblychilepas platyactis	MCZ 380752	South Africa	MK322205	MK322205	MK322205	MK331037	MK331633	MK331633	MK291133	MK322110	MK291063
Amblychilepas sp.1	MNHN 2013 363	Papua New Guinea	MK322237	MK322237	MK322237	MK331047	MK331664	MK331664	MK291137	MK322103	MK291056
Dendrofissurella scutellum	MCZ 378357	South Africa	MK322178	MK322178	MK322178	MK331035	MK331610	MK331610	MK291131	MK322104	MK291061
Dendrofissurella scutellum	MCZ 378358	South Africa	MK322179	MK322179	MK322179	MK331036	MK331117	–	MK291132	HM771550	MK291062
Fissurella barbadensis	MCZ 378449	Bahamas	HM771465	HM771465	HM771465	HM771511	HM771511	HM771511	HM771593	HM771553	HM771627
Fissurella cf. angusta	MCZ 378446	Bahamas	HM771468	HM771468	HM771468	HM771514	–	–	HM771596	MK322111	HM771630
Fissurella clenchi	MZSP 104483	Brazil	MK322247	MK322247	MK322247	MK331042	MK331673	MK331673	MK291141	MK322108	MK291076
Fissurella cumingi	MCZ 378452	Chile	MK322192	MK322192	MK322192	MK331044	MK331622	MK331622	MK291127	MK322109	–
Fissurella latimarginata	MCZ 381347	Chile	MK322210	MK322210	MK322210	MK331043	–	–	MK291129	–	–
Fissurella mutabilis	MCZ 378468	South Africa	MK322196	MK322196	MK322196	MK331031	MK331625	MK331625	MK291134	–	–
Fissurella natalensis	MCZ 378455_2	South Africa	MK322193	MK322193	MK322193	MK331033	MK331623	MK331623	MK291135	–	MK291060
Fissurella nodosa	MCZ 378456	Bahamas	FJ977640	FJ977640	FJ977640	FJ977671	FJ977671	FJ977671	FJ977732	FJ977703	FJ977756

Table 1 (continued)

Species	Voucher	Country	18Sa rRNA	18Sb rRNA	18Sc rRNA	28Sa rRNA	28Sb rRNA	28Sc rRNA	H3	16S rRNA	COI
Fissurella nubecula	MCZ 378463	Spain	HM771464	HM771464	HM771464	HM771510	HM771510	HM771510	HM771592	HM771549	HM771626
Fissurella rosea	MZSP 113112	Brazil	MK322250	MK322250	MK322250	MK331041	MK331675	MK331675	MK291142	MK322112	MK291077
Fissurella sp.	MCZ 378467_1	Costa Rica	MK322195	MK322195	MK322195	–	–	–	MK291140	MK322113	–
Fissurella sp.1	MNHN 2009 25069	Mozambique	MK322222	MK322222	MK322222	MK331032	MK331650	MK331650	–	MK322105	–
Fissurella sp.1	MNHN 2009 25077	Mozambique	MK322223	MK322223	MK322223	MK331038	MK331651	MK331651	–	MK322106	–
Fissurella sp.7	MNHN 2009 25116	Senegal	MK331687	–	MK331697	MK331045	MK331652	MK331652	–	–	–
Fissurella virescens	MCZ 378466_2	Costa Rica	MK322194	MK322194	MK322194	MK331040	MK331624	MK331624	MK291136	MK322114	–
Lucapinella sp.2	MNHN 2009 25059	Mozambique	MK322220	MK322220	MK322220	MK331049	MK331648	MK331648	MK291139	MK322099	MK291055
Macroschisma elegans	MNHN 2009 14321	Madagascar	MK322219	MK322219	MK322219	–	MK331646	MK331646	MK291146	MK322098	MK291057
Macroschisma sp.	MNHN 2013 14887	Papua New Guinea	MK331688	–	MK331698	MK331046	MK331111	–	MK291138	MK322100	–
Medusafissurella dubia	NMP L8258	Mozambique	MK331685	–	MK331707	–	MK331106	MK331106	MK291143	–	–
Medusafissurella sp.	MNHN 2009 25053	Mozambique	MK331686	–	MK331699	MK331034	MK331647	MK331647	MK291144	MK322107	–
Zeidorinae											
Cornisepta cf. rostrata	MNHN 2009 20720	French Polynesia	–	MK322177	MK331706	–	MK331099	–	MK291118	–	–
Cornisepta crossei	MCZ 378337	Spain	MK322177	MK322177	MK322177	–	MK331108	–	MK291119	–	–
Hemimarginula pumila	MZSP 115402_1	Brazil	MK322251	MK322251	MK322251	–	MK331112	MK331112	MK291125	–	MK291073
Hemimarginula pumila	MCZ 378416	Panama	MK322190	MK322190	MK322190	MK331094	MK331102	MK331102	MK291124	–	MK291074
Hemimarginula sp.1	MNHN 2013 17277	Papua New Guinea	MK322230	MK322230	MK322230	MK331097	MK331120	–	MK291191	MK322145	MK291075
Hemimarginula sp.2	MNHN 2013 5916	Papua New Guinea	MK322242	MK322242	MK322242	MK331095	MK331109	–	MK291123	MK322144	MK291079
Hemitoma octoradiata	MZSP 111522	Brazil	MK322249	MK322249	MK322249	–	MK331109	–	MK291122	–	MK291072
Hemitoma octoradiata	MCZ 382638	Panama	–	MK331682	MK331682	–	MK331101	–	MK291121	MK322143	–
Montfortista kirana	MNHN 2007 33464	Philippines	–	–	MK331708	–	MK331098	–	MK291187	–	MK291081
Montfortista oldhamiana	MNHN 2013 17416	Papua New Guinea	MK322231	MK322231	MK322231	MK331096	–	MK331125	MK291186	–	MK291071
Profundisepta aff. profundi	MNHN 2007 38845	French Polynesia	MK331693	–	MK331701	–	MK331104	–	–	–	MK291010
Profundisepta aff. profundi	MNHN 2009 20735	French Polynesia	MK331694	–	MK331702	–	MK331100	–	–	–	MK291011
Puncturella cf. regia	AORI_YK2589	Japan	MK322152	MK322152	MK322152	MK331083	MK331589	MK331589	MK291112	MK322053	–
Puncturella aff. corolla	MNHN 2013 56380	French Guiana	MK322240	MK322240	MK322240	MK331085	MK331666	MK331666	MK291111	MK322054	–
Puncturella aff. corolla	MNHN 2007 34775	Philippines	MK322216	MK322216	MK322216	MK331084	MK331643	MK331643	MK291110	MK322052	–
Puncturella cucullata*	MCZ 378339	USA	GQ160793	GQ160793	GQ160793	GQ160641	GQ160641	GQ160641	GQ160727	GQ160688	GQ160755
Puncturella dorcas	AORI_YK2590	Japan	MK322153	MK322153	MK322153	MK331087	MK331113	–	MK291107	MK322059	MK291007
Puncturella pelex*	AORI_YK2594	Japan	MK322156	MK322156	MK322156	MK331088	MK331114	–	MK291108	MK322060	MK291008
Puncturella pileolus*	MNHN 2007 31364	Solomon Islands	MK322212	MK322212	MK322212	MK331089	MK331640	MK331640	–	–	MK291009
Puncturella sp.	MCZ 381308	Australia	MK331692	–	MK331703	MK331079	MK331607	MK331607	MK291113	MK322064	MK290999
Puncturella sp.	MCZ 376616	Greenland	MK322174	MK322174	MK322174	MK331082	MK331629	MK331629	MK291103	MK322061	MK290995
Puncturella sp.	MCZ 378697	USA	MK322201	MK322201	MK322201	MK331086	MK331653	MK331653	MK291114	MK322062	MK290996
Puncturella sp.1	MNHN 2009 26304	New Caledonia	MK322224	MK322224	MK322224	MK331081	MK331663	MK331663	MK291106	MK322063	MK291006
Puncturella sp.3	MNHN 2013 18667	Papua New Guinea	MK322235	MK322235	MK322235	MK331091	MK331642	MK331642	MK291190	MK322056	MK290997
Puncturella sp.3	MNHN 2007 31494	Philippines	MK322214	MK322214	MK322214	MK331090	MK331119	–	–	–	MK291003
Puncturella sp.4	MNHN 2013 19868	Papua New Guinea	MK322236	MK322236	MK322236	–	MK331590	MK331590	MK291104	MK322058	MK291002
Puncturella sp.A	AORI_YK2591	Japan	MK322154	MK322154	MK322154	MK331092	MK331591	MK331591	MK291109	MK322057	MK291005
Puncturella sp.B	AORI_YK2593	Philippines	MK322155	MK322155	MK322155	MK331080	MK331116	–	MK291105	MK322065	MK291004
Puncturella sp.C	AORI_YK2619	Japan	MK322169	MK322169	MK322169	–	MK331105	–	MK291116	–	MK290998
Puncturella spirigera	MNHN 2009 7905	Antarctica	MK331690	–	MK331704	–	–	–	MK291117	–	MK291000
Puncturella spirigera	MNHN 2009 8149	Antarctica	MK331691	–	MK331705	–	MK331655	MK331655	MK291115	MK322048	MK291001
Zeidora sp.	MNHN 2013 7769	Guadeloupe	MK331684	–	–	MK330997	–	MK331123	MK291082	–	–
Rimulinae											
Rimula cumingii	AORI_YK2618	Japan	MK322168	MK322168	MK322168	MK331093	MK331602	MK331602	MK291126	MK322051	MK290994
Rimula exquisita	AORI_YK194	Japan	MK322150	MK322150	MK322150	–	MK331587	MK331587	AB365263	MK322050	AB365214
Rimula sp.	MNHN 2013 9217	Guadeloupe	MK322245	MK322245	MK322245	–	MK331672	MK331672	MK291193	MK322049	MK290993

Table 1 (*continued*)

Species	Voucher	Country	18Sa rRNA	18Sb rRNA	18Sc rRNA	28Sa rRNA	28Sb rRNA	28Sc rRNA	H3	16S rRNA	COI
Outgroups											
Cocculina cf. japonica	MNHN 2013 41045	Papua New Guinea	–	MK331683	MK331683	–	–	MK331128	–	MK322142	MK291078
Haliotis corrugata	MCZ 378483	USA	FJ977644	FJ977644	FJ977644	FJ977675	FJ977675	FJ977675	FJ977736	FJ977707	FJ977760
Lepetodrilus elevatus	MCZ 378530	9North EPR	DQ093432	DQ093432	DQ093432	GQ160654	GQ160654	GQ160654	DQ093501	DQ093475	DQ093520
Entemnotrochus adansonianus	MCZ 378426	N/A	AF120509	AF120509	AF120509	FJ977667	FJ977667	FJ977667	AY377774	AY377621	L78910
Anatoma sp.	N/A	N/A	AB365302	AB365302	AB365302	–	–	–	AB365260	–	AB365210
Sinezona confusa	N/A	N/A	AF120512	AF120512	AF120512	DQ279981	DQ279981	DQ279981	AY377773	AY377620	AF120631
Bathymargarites symplector	MCZ 378256	9North EPR	DQ093433	DQ093433	DQ093433	GQ160653	GQ160653	GQ160653	DQ093503	DQ093477	DQ093521
Cittarium pica	MCZ 378303	Bahamas	FJ977646	FJ977646	FJ977646	FJ977677	FJ977677	FJ977677	FJ977738	FJ977709	FJ977761
Homalopoma picta	MCZ 378510	French Polynesia	GQ160799	GQ160799	GQ160799	–	GQ160648	–	GQ160734	GQ160694	GQ160759
Lithopoma phoebium	MCZ 378246	Bahamas	FJ977649	FJ977649	FJ977649	FJ977680	FJ977680	FJ977680	FJ977741	FJ977712	FJ977762

concatenated with Phyutility 2.2.6 (Smith and Dunn, 2008). We defined the partitioning scheme and selected the best model of sequence evolution for each partition with the modified Akaike Information Criterion (AICc) in PartitionFinder 2.1.1 (Lanfear et al., 2016). There were seven resulting partitions, one for each of the five genes plus the separation of the 3rd codon position of COI and histone H3. From the models available for MrBayes or RAxML, the resulting model was GTR + G for all partitions; we disregarded options with + I for invariant sites since across-site heterogeneity is already accounted for by the gamma distribution (Yang, 2014). The partitioned matrix was analyzed in MrBayes 3.2.5 (Huelsenbeck and Ronquist, 2001) for over 19 million generations with convergence assessed in Tracer 1.7 (Rambaut et al., 2018), and in RAxML 8.2.10 (Stamatakis, 2014) with the -autoMRE bootstrap option. All alignments and trees are available in the Supplementary Material. Tree figures were edited with the R package ggtree 1.13.0 (R Core Team, 2019; Yu et al., 2017).

2.4. Divergence time analyses

For divergence time estimation, we used two methods implemented in MrBayes: (1) traditional node dating with a birth-death tree prior and constraints on specific nodes (ND), and (2) tip dating with a fossilized birth-death tree prior (FBD) allowing for sampled ancestor–descendant relationships (Gavryushkina et al., 2014; Heath et al., 2014). We compiled information from direct observation of fissurellid fossils from the MCZ and from specimens for which images were available for identification in the database of the MNHN. We further obtained fossil age data from the oldest fossils for each subfamily from the Paleobiology Database (https://paleobiodb.org), conditional on identification being possible from images in the reference publications. Because we were interested in deep divergences in the tree, no fossils more recent than the Paleogene (23 Ma) were considered.

For the FBD model, 51 fossils were given as tips in the tree with their most accurate clade assignment in partial constraints. Fossils were assigned to a specific clade, but some were identified to belong to a non-monophyletic taxon (e.g., genus *Emarginula*). In these cases, the fossils were assigned to the most inclusive clade to which they belong, excluding specific subclades to which they definitely do not belong, and therefore averaging over the uncertainty of the identification and allowing for their position as either crown or stem fossils (see Table 3 for more details). Tip ages were given as uniform distributions with the ranges of their correspondent geological stages (taken from the Chronostratigraphic Chart v2018/08 from the International Commission on Stratigraphy). Contrary to the FBD model, the node dating approach (ND) requires the ages of calibrated nodes to be constrained with a prior distribution. Because of that, only the oldest fossil for any given node can be used, limiting the number of fossils in the analysis. For ND, we used 6 fossil age calibrations (Table 3). Each calibrated node was assigned an offset log-normal prior distribution with offset equal to the lower boundary of the geological stage of the fossil, mean of 15 million years and standard deviation of 2 million years.

We placed an exponential(20) prior on speciation rate, a beta(1,1) prior on extinction rate, and a sample probability of 0.07 for extant tips – an approximation of the proportion of sampled species over the total estimated diversity of the family (considering that ∼75% of mollusk diversity is estimated to be undescribed (Bouchet et al., 2016)). For ND, we placed a random prior on the taxon sampling strategy and a fixed(0) prior on the fossilization rate, so that no fossilization was accounted for in the ND analysis. For FBD, we set the fossilization prior to beta(1,15), and the species sampling strategy to random 1: 23 0, indicating that no fossils were sampled earlier than 23 Ma. For the uncorrelated relaxed molecular clock (IGR), we placed an exponential(1000) on the clock rate prior, and an exponential(50) on the variance of the gamma distribution.

Basal nodes that were recovered in all topological analyses and were well supported in the Bayesian inference topology were constrained as
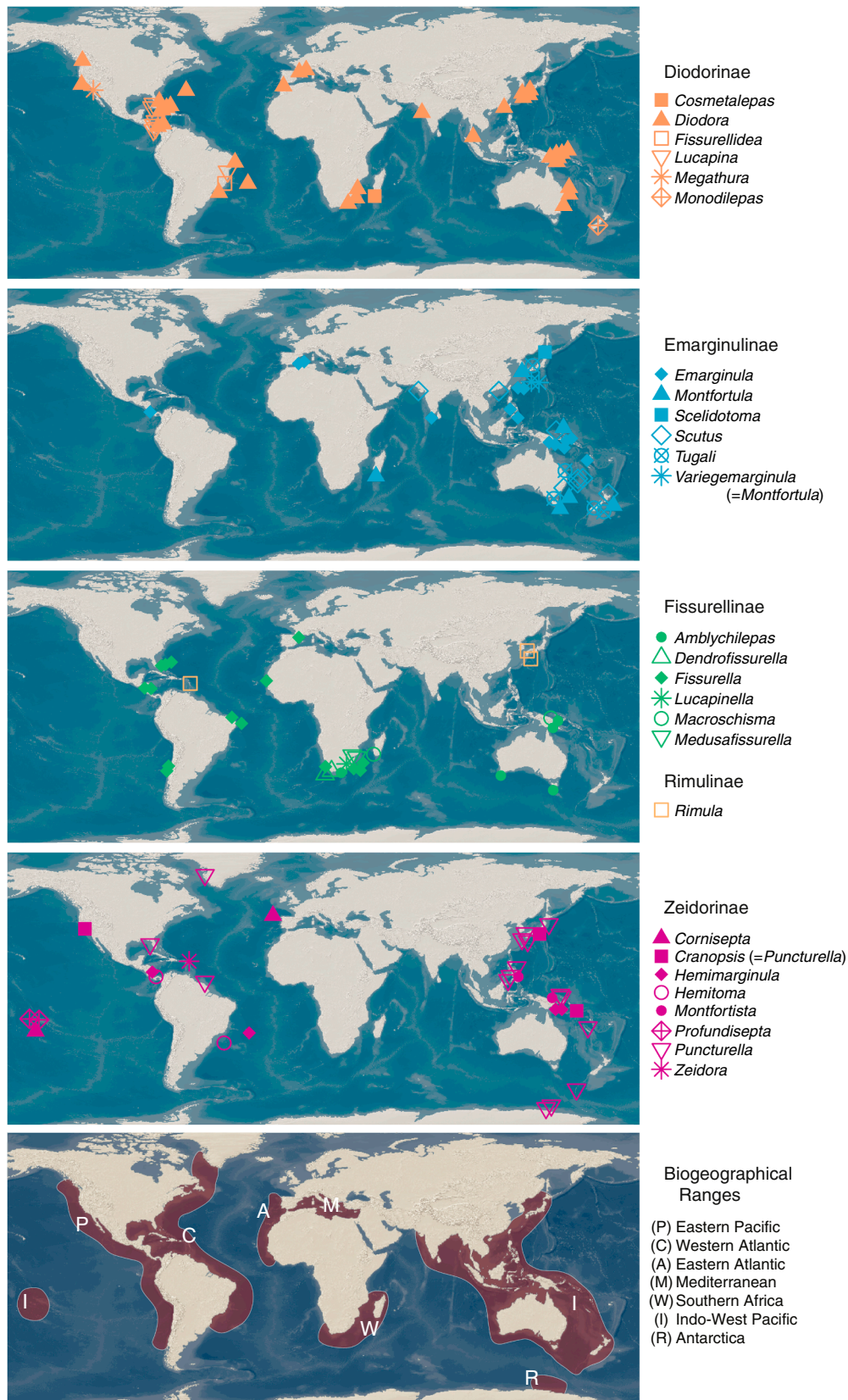
Fig. 1. Distribution of sampled Fissurellidae and defined ranges for biogeographical analyses. Colors follow subfamily designation in the rest of the article and shapes represent genera within each subfamily. A small jitter was added to coordinates to minimize overlap of points in the same locality. Base map from Natural Earth (http://naturalearthdata.com).

Table 2
Primer sequences and annealing temperatures used for amplification and sequencing.

Primer		Sequence		Reference	Annealing Temperature
18Sa	1F	5′-TACCTGGTTGATCCTGCCAGTAG-3′	F	Giribet et al. (1996)	47 °C
	4R	5′-GAATTACCGCGGCTGCTGG-3′	R	Giribet et al. (1996)	
18Sb	3F	5′-GTTCGATTCCGGAGAGGGA-3′	F	Giribet et al. (1996)	54 °C
	bi	5′-GAGTCTCGTTCGTTATCGGA-3′	R	Whiting et al. (1997)	
18Sc	a2.0	5′-ATGGTTGCAAAGCTGAAAC-3′	F	Whiting et al. (1997)	47 °C
	9R	5′-GATCCTTCCGCAGGTTCACCTAC-3′	R	Giribet et al. (1996)	
28Sa	rd1a	5′-CCCSCGTAAYTTAGGCATAT-3′	F	Edgecombe and Giribet (2006)	47 °C
	rd4b	5′-CCTTGGTCCGTGTTTCAAGAC -3′	R	Edgecombe and Giribet (2006)	
28Sb	a	5′-GACCCGTCTTGAAACACGGA-3′	F	Whiting et al. (1997)	54 °C
	rd5b	5′-CCACAGCGCCAGTTCTGCTTAC-3′	R	Schwendinger and Giribet (2005)	
28Sc	rd4.8a	5′-ACCTATTCTCAAACTTTAAATGG-3′	F	Schwendinger and Giribet (2005)	47 °C
	rd7b1	5′-GACTTCCCTTACCTACAT-3′	R	Schwendinger and Giribet (2005)	
H3	H3F	5′-ATGGCTCGTACCAAGCAGACVGC-3′	F	Colgan et al. (1998)	54 °C
	H3R	5′-ATATCCTTRGGCATRATRGTGAC-3′	R	Colgan et al. (1998)	
16S	a	5′-CGCCTGTTTATCAAAAACAT-3′	F	Palumbi (1996)	47 °C
	b	5′-CTCCGGTTTGAACTCAGATCA-3′	R	Palumbi (1996)	
COI	LCO1490	5′-GGTCAACAAATCATAAAGATATTGG-3′	F	Folmer et al. (1994)	47 °C
	HCO2198	5′-TAAACTTCAGGGTGACCAAAAAATCA-3′	R	Folmer et al. (1994)	
	HCOout	5′-CCAGGTAAAATTAAAATATAAACTTC-3′	R	Carpenter and Wheeler (1999)	
	HCOoutout	5′-GTAAATATATGRTGDGCTC-3′	R	Prendini et al. (2005)	
	dgLCO1490	5′-GGTCAACAAATCATAAAGAYATYGG-3′	F	Meyer (2003)	
	dgHCO2198	5′-TAAACTTCAGGGTGACCAAARAAYCA-3′	R	Meyer (2003)	
	jgLCO1490	5′-TITCIACIAAYCAYAARGAYATTGG-3′	F	Geller et al. (2013)	
	jgHCO2198	5′-TAIACYTCIGGRTGICCRAARAAYCA-3′	R	Geller et al. (2013)	

monophyletic (list of constraints available in the nexus file in the Supplementary Material). For each dating method, two sets of analyses were run with identical settings except for the inclusion of one fossil. The oldest fossil widely accepted as a fissurellid is *Emarginula muensteri* Pictet, 1855 from the Triassic (Geiger et al., 2008), therefore one set of analyses used its age as the oldest record (Triassic-ND, Triassic-FBD). However, there is also a fossil described as *Retshitsella egorovi* Mazaev, 1998 from the Carboniferous assigned to the family (Mazaev, 1998). Photos from the original publication indeed indicate it is a fissurellid, although confirmation and a more specific assignment is not possible without a close examination of the fossil. Therefore, we ran a second set of analyses with all the same fossils and calibrations, plus this older fossil age to calibrate the family (Carboniferous-ND, Carboniferous-FBD). The tree age prior was set to a uniform distribution between 252 and 426 Ma (Triassic-FBD), or between 319 and 426 Ma (Carboniferous-FBD). The minimum bound corresponds to the age of the oldest fossil plus 15 million years, while 426 Ma is the estimated maximum age of Vetigastropoda in Zapata et al. (2014).

For each combination of calibration method and oldest fossil, we ran four independent runs of four chains for over 300 million generations sampling every 10,000 steps until the average standard deviation of split frequencies was below 0.02 and parameters of the model reached convergence as assessed for the combined chains in Tracer. Due to the large number of generations recorded in each analysis, we subsampled the posterior distribution of trees with a custom python script (*get_posterior_trees.py*), retaining ten thousand interspaced samples after discarding the burn-in. For the FBD trees, this script also pruned fossil taxa. We then summarized the results with a maximum clade credibility tree with median heights in TreeAnnotator 2.4.7 (Drummond et al., 2012). For each analysis we also ran MrBayes without the data to check the effects of the priors (summary results in the Supplementary Material). The custom script and an input nexus file with parameters for all dating analyses is deposited in the Supplementary Material.

2.5. Biogeographic analyses

We inferred ancestral areas in the fissurellid phylogeny with a model-based approach in the R package BioGeoBEARS 1.1.2 (Matzke, 2014, 2013). We defined seven geographic ranges based on the current distribution of the family and on delimited marine biogeographical

areas (Costello et al., 2017): Eastern Pacific (P), Western Atlantic (C), Eastern Atlantic (A), Mediterranean (M), Southern Africa (W), Indo-West Pacific (I) and Antarctica (R) (Fig. 1). Ancestral areas could then be estimated as combinations of these seven areas by BioGeoBEARS. The maximum range size was set to 3, which to our knowledge is the maximum number of areas in which any extant fissurellid in our analyses is present. The distribution for identified species was primarily taken from OBIS (http://www.iobis.org); when no records were found for a given species, we also checked WoRMS (http://www.marinespecies.org). Outlier records that could not be confirmed from published references were disregarded. Terminals identified to genus but not species were assigned their collecting locality for a conservative estimate of the distribution, instead of using the more widespread range of the entire genus. Three biogeographic models implemented in BioGeoBEARS were compared, namely the dispersal-extinction-cladogenesis (DEC) model (Ree and Smith, 2008), a maximum likelihood version of the dispersal-vicariance (DIVAlike) model (Ronquist, 1997) and a likelihood version of the Bayesian biogeographic inference with no-cladogenesis (BAYAREAlike) model (Landis et al., 2013). We further accounted for jump dispersal/founder-event speciation by implementing these three models with the additional parameter j (Matzke, 2014), for a total of six models (DEC, DEC + j, DIVAlike, DIVAlike + j, BAYAREAlike, BAYAREAlike + j). Biogeographical analyses were based on the calibrated Triassic-FBD tree. Analyses based on the alternative chronograms are in the Supplementary Material. We used the modified Akaike Information Criterion (AICc) to select the model that best fit the data. The script for this analysis is available in the Supplementary Material and was based on examples from Matzke (2015).

The time and geographical distribution of fissurellid fossils was assessed with maps from the Paleobiology Database Navigator (https://paleobiodb.org/navigator) as a second line of evidence about the routes of oceanic dispersal.

3. Results

3.1. Phylogenetic relationships

Bayesian inference (BI) and maximum likelihood (ML) resulted in the same overall topology (Fig. 2, Supplementary Material); none of the relationships that differed between trees were well supported and these

Table 3
Fossil specimens used in the dating analyses. Museum of Comparative Zoology, Invertebrate Paleontology (MCZ IPGA); Muséum National d'Histoire Naturelle (MNHN.F); Paleobiology Database (PaleoDB, http://paleodb.org). Fossil information can be found in the links. Fossils in bold are the earliest known records of clades used for node calibrations on the node dating analyses (ND).

Catalog Number	Taxon Identification from Source	Country	Geological Stage	Stratigraphic Age Range (Ma)	Our Identification	Clade Assignment for Dating Analyses	Reference
PaleoDB collection 154864	***Retshitsella egorovi***	**Russia**	**Gzhelian**	**298.9–303.7**	**Fissurellidae**	**Fissurellidae, but not (Diodorinae, Fissurellinae)**	Mazaev (1998)
PaleoDB collection 144631	***Emarginula muensteri***	**Italy**	**Carnian**	**227–237**	**Fissurellidae**	**Fissurellidae, but not (Fissurellinae, Diodorinae)**	Kittl (1891)
MNHN.F.J08529	*Emarginula blotii*	France	Bathonian	166.1–168.3	Fissurellidae	Fissurellidae, but not (Diodorinae, Fissurellinae)	Cossmann (1885a)
MNHN.F.J08527	*Rimula clathrata*	France	Bathonian	166.1–168.3	Fissurellidae	Fissurellidae, but not (Diodorinae, Fissurellinae)	Cossmann (1885a)
MNHN.F.A26135	*Rimula cornucopiae*	France	Oxfordian	157.3–163.5	Fissurellidae	Fissurellidae, but not (Emarginulinae, (Fissurellinae, Diodorinae))	Maire (1927)
MNHN.F.A26134	*Rimula paucicostata*	France	Oxfordian	157.3–163.5	Fissurellidae	Fissurellidae, but not (Emarginulinae, (Fissurellinae, Diodorinae))	Maire (1927)
PaleoDB collection 176994	*? Rimula* sp.	Denmark	Danian	61.6–66	Fissurellidae	Fissurellidae	Lauridsen and Schnetler (2014)
PaleoDB collection 22931	***Rimula praeintorta***	**Belgium**	**Danian**	**61.6–66**	***Rimula***	***Rimula***	Cossmann (1913); Glibert (1973)
MNHN.F.J01981	*Rimula defrancei*	France	Lutetian	41.2–47.8	*Rimula*	*Rimula*	Cossmann and Pissarro (1913); Le Renard and Pacaud (1995)
MNHN.F.A53001	*Rimula (Semperia) houdasi*	France	Bartonian	37.8–41.2	*Rimula*	*Rimula*	Cossmann (1922)
PaleoDB collection 178748	***Hemitoma (Montfortia) cantonensis***	**USA**	**Ypresian**	**47.8–56**	***Montfortista***	***Montfortista***	Squires (1987)
MNHN.F.A53000	*Subemarginula polygonalis*	France	Bartonian	37.8–41.2	*Montfortia*	*Montfortista*	Cossmann (1922)
PaleoDB Collection 6267	***Puncturella caninata***	**Australia**	**Thanetian**	**56–59.2**	***Puncturella***	***Puncturella***	Darragh (1997)
MNHN.F.J01980	*Emarginula clypeata*	France	Lutetian	41.2–47.8	*Zeidora*	*Zeidora*	Cossmann and Pissarro (1913); Le Renard and Pacaud (1995)
MNHN.F.J01988	*Emarginula clypeata*	France	Lutetian	41.2–47.8	*Zeidora*	*Zeidora*	Cossmann and Pissarro (1913); Le Renard and Pacaud (1995)
MNHN.F.A24934	*Emarginula neocomiensis*	France	Hauterivian	129.4–132.9	*Emarginula*	(Emarginulinae, (Fissurellinae, Diodorinae)), but not (Diodorinae, Fissurellinae)	Kollmann (2005)
MNHN.F.S06353	*Emarginula neocomiensis*	France	Hauterivian	129.4–132.9	*Emarginula*	(Emarginulinae, (Fissurellinae, Diodorinae)), but not (Diodorinae, Fissurellinae)	Kollmann (2005)
MNHN.F.R10038	*Emarginula pelagica*	France	Cenomanian	93.9–100.5	*Emarginula*	(Emarginulinae, (Fissurellinae, Diodorinae)), but not (Diodorinae, Fissurellinae)	D'Orbigny (1842); Kollmann (2005)
MNHN.F.J08871	*Emarginula arnaudi*	France	Campanian - Maastrichtian	66–83.6	*Emarginula*	(Emarginulinae, (Fissurellinae, Diodorinae)), but not (Diodorinae, Fissurellinae)	Termier (1954)
MNHN.F.J03325	*Emarginula gigantea*	France	Campanian - Maastrichtian	66–83.6	*Emarginula*	(Emarginulinae, (Fissurellinae, Diodorinae)), but not (Diodorinae, Fissurellinae)	Termier (1954)
MNHN.F.J05433	*Clypidina celinae*	France	Danian	61.6–66	Emarginulinae	(Emarginulinae, (Fissurellinae, Diodorinae)), but not (Diodorinae, Fissurellinae)	(Pacaud, 2004)
MNHN.F.R63409	*Emarginula cavernosa*	France	Danian	61.6–66	*Emarginula*	(Emarginulinae, (Fissurellinae, Diodorinae)), but not (Diodorinae, Fissurellinae)	Pacaud (2004)

Table 3 (*continued*)

| Catalog Number	Taxon Identification from Source	Country	Geological Stage	Stratigraphic Age Range (Ma)	Our Identification	Clade Assignment for Dating Analyses	Reference
MNHN.F.J05457	*Emarginula coralliora*	France	Danian	61.6–66	*Emarginula*	(Emarginulinae, (Fissurellinae, Diodorinae)), but not (Diodorinae, Fissurellinae)	Pacaud (2004)
MNHN.F.J02050	*Emarginula costata*	France	Lutetian	41.2–47.8	*Emarginula*	(Emarginulinae, (Fissurellinae, Diodorinae)), but not (Diodorinae, Fissurellinae)	Cossmann and Pissarro (1913); Le Renard and Pacaud (1995)
MCZ IPGA-28687	*Emarginula arata*	USA	Bartonian	37.8–41.2	Emarginulinae	(Emarginulinae, (Fissurellinae, Diodorinae)), but not (Diodorinae, Fissurellinae)	
MNHN.F.J01982	*Emarginula auversiensis*	France	Bartonian	37.8–41.2	*Emarginula*	(Emarginulinae, (Fissurellinae, Diodorinae)), but not (Diodorinae, Fissurellinae)	Cossmann and Pissarro (1913); Le Renard and Pacaud (1995)
MNHN.F.J04693	*Emarginula clathrata*	France	Bartonian	37.8–41.2	*Emarginula*	(Emarginulinae, (Fissurellinae, Diodorinae)), but not (Diodorinae, Fissurellinae)	Cossmann (1902)
MNHN.F.J05288	*Emarginula conformis*	France	Rupelian	27.82–33.9	*Emarginula*	(Emarginulinae, (Fissurellinae, Diodorinae)), but not (Diodorinae, Fissurellinae)	Cossmann and Lambert (1884); Lozouet et al. (2012)
MCZ IPGA-10859	*Emarginula schlottheimii*	Germany	Chattian	23.03–27.82	*Emarginula*	(Emarginulinae, (Fissurellinae, Diodorinae)), but not (Diodorinae, Fissurellinae)	
MNHN.F.J01960	***Emarginula compressa***	**France**	**Lutetian**	**41.2–47.8**	***Montfortula***	***Montfortula***	Cossmann (1888, 1885b)
MNHN.F.J11257	*Submarginula defrancei*	France	Lutetian	41.2–47.8	*Montfortula*	*Montfortula*	Cossmann (1904); Cossmann and Pissarro (1902); Tréguier et al. (2017)
MNHN.F.R53068	*Clypidina defrancei*	France	Bartonian	37.8–41.2	*Montfortula*	*Montfortula*	Ters (1982)
MNHN.F.A53118	*Montfortula defrancei*	France	Bartonian	37.8–41.2	*Montfortula*	*Montfortula*	Lebrun et al. (2012)
MNHN.F.J05459	*Diodora sp.*	France	Danian	61.6–66	(Diodorinae, Fissurellinae)	(Diodorinae, Fissurellinae)	Pacaud (2004)
PaleoDB collection 7791	*Fissurella migeriensis*	Nigeria	Selandian	59.2–61.6	(Diodorinae, Fissurellinae)	(Diodorinae, Fissurellinae)	(Adegoke, 1977)
PaleoDB collection 22931	*Diodora concentrica*	Belgium	Danian	61.6–66	*Diodora*	Diodorinae	Cossmann (1913); Gilbert (1973)
MNHN.F.R63294	***Diodora cormeti***	**France**	**Danian**	**61.6–66**	***Diodora***	**Diodorinae**	Pacaud (2004)
PaleoDB collection 22931	*Diodora dolloi*	Belgium	Danian	61.6–66	*Diodora*	Diodorinae	Cossmann (1913); Gilbert (1973)
MNHN.F.J01940	*Fissurella cossmanni*	France	Thanetian	56–59.2	*Diodora*	Diodorinae	Cossmann (1907); Cossmann and Pissarro (1913); Le Renard and Pacaud (1995); Pacaud (2004)
MNHN.F.A24997	*Diodora squamosa*	France	Lutetian	41.2–47.8	*Diodora*	Diodorinae	Caze et al. (2012); Merle et al. (2008)
MNHN.F.J01944	*Fissurella asperrima*	France	Lutetian	41.2–47.8	*Diodora*	Diodorinae	Cossmann and Pissarro (1913); Le Renard and Pacaud (1995)
MNHN.F.J05409	*Fissurella brasili*	France	Lutetian	41.2–47.8	*Diodora*	Diodorinae	Cossmann and Pissarro (1905)
MNHN.F.B56206	*Fissurella cycloides*	France	Lutetian	41.2–47.8	Diodorinae	Diodorinae	Cossmann and Pissarro (1905)
MNHN.F.J01946	*Fissurella distans*	France	Lutetian	41.2–47.8	*Diodora*	Diodorinae	Cossmann and Pissarro (1913); Le Renard and Pacaud (1995)
MNHN.F.J11151	*Fissurella imbrex*	France	Lutetian	41.2–47.8	*Diodora*	Diodorinae	Cossmann and Pissarro (1913); Le Renard and Pacaud (1995)
MCZ IPGA-28166	*Fissuridea labiata*	France	Lutetian	41.2–47.8	*Diodora*	Diodorinae	
PaleoDB collection 4900	*? Megathura sp.*	USA	Middle Eocene	37.2–48.6	Diodorinae	Diodorinae	Lindberg and Squires (1990); Vasseur (1917, 1881)
MNHN.F.J03907	*Fissurella bezanconi*	France	Bartonian	37.8–41.2	Diodorinae	Diodorinae	Cossmann (1888, 1886); Cossmann and Pissarro (1913); Le Renard and Pacaud (1995)
MNHN.F.J01939	*Fissurella chevallieri*	France	Bartonian	37.8–41.2	*Diodora*	Diodorinae	
MNHN.F.J01942	*Fissurella decisa*	France	Bartonian	37.8–41.2	*Diodora*	Diodorinae	Cossmann and Pissarro (1913); Le Renard and Pacaud (1995)
MCZ IPGA-28544	*Fissurella tenebrosa*	USA	Bartonian	37.8–41.2	*Diodora*	Diodorinae	
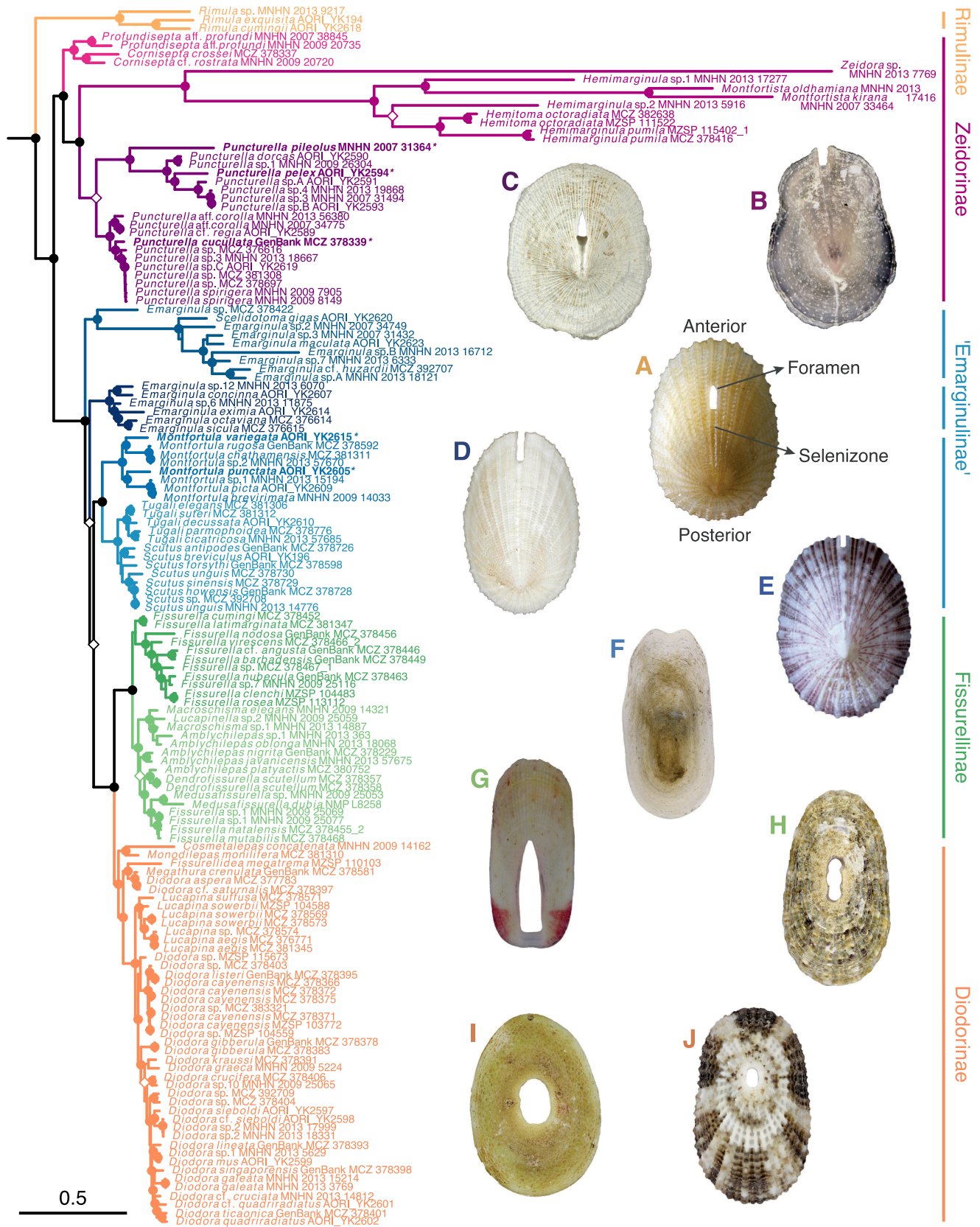
Fig. 2. Fissurellid phylogeny from Bayesian inference. Filled circles indicate PP > 0.95, open diamonds indicate PP > 0.90. New synonyms are in bold and marked with an asterisk (*Variegemarginula* **syn. nov.** of *Montfortula*; *Cranopsis* **syn. nov.** of *Puncturella*). A, *Rimula exquisita* AORI_YK 194; B, *Hemimarginula* sp.2 MNHN 2013 5916; C, *Puncturella corolla* MNHN 2007 34775; D, *Emarginula* sp.3 MNHN 2007 31432; E, *Montfortula variegata* AORI_YK 2615; F, *Scutus unguis* MNHN 2013 14776; G, *Macroschisma elegans* MNHN 2009 14321; H, *Fissurella* sp.1 MNHN 2009 25069; I, *Cosmetalepas concatenata* MNHN 2009 14162; J, *Diodora* sp.1 MNHN 2013 5929. Photos by Yasunori Kano (A, E), Tauana Cunha (B, F-J) and Yves Terryn (C, D).
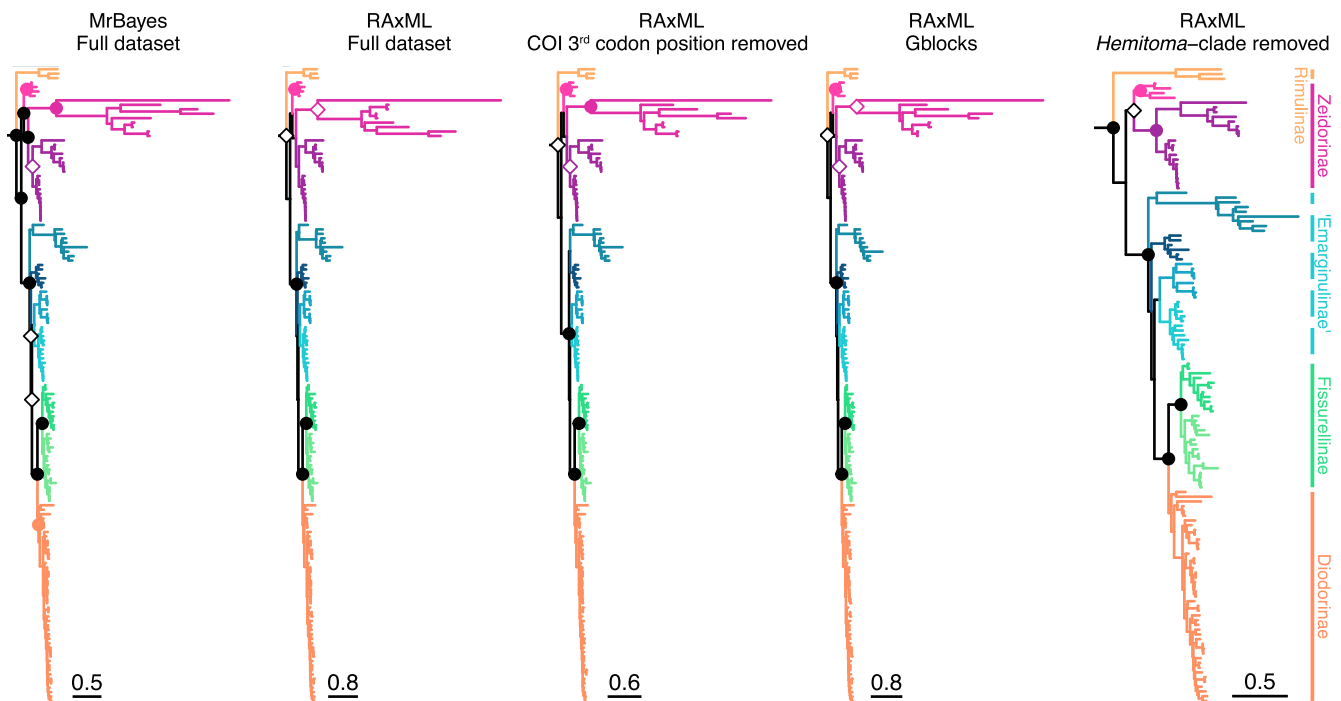
Fig. 3. Comparison of the support at basal nodes on full datasets analyzed with Bayesian inference and maximum likelihood, and three reduced ML datasets: without the 3rd codon position of COI, trimmed with Gblocks, and without the long branch leading to *Hemitoma* and related genera. Filled circles indicate PP > 0.95 or BS > 85, open diamonds indicate PP > 0.90 or BS > 70. The only nodes being evaluated are the ones with either a circle or a diamond on the Bayesian tree.

were restricted to closely related taxa. The following description corresponds to the results of the BI, with the only differences to the ML tree being the support values. Three of the four accepted fissurellid subfamilies were recovered as monophyletic with high posterior probability (PP): Hemitominae, Fissurellinae J. Fleming, 1822, and Diodorinae Odhner, 1932 (Fig. 2). The traditional subfamily Emarginulinae, present in nearly all classifications ever proposed for fissurellids, was not monophyletic. Instead, three smaller lineages were recovered as a grade with lower support (Fig. 2).

A few genera previously considered part of the subfamily Emarginulinae – *Hemitoma* Swainson, 1840, *Puncturella* R. T. Lowe, 1827, and *Cranopsis* A. Adams, 1860 – had already been recovered as Hemitominae by Aktipis et al. (2011). Because this placement was questioned due to the long branch of *Hemitoma* and the morphological and ecological differences among them (Aktipis et al., 2011; McLean, 2011), we sequenced new specimens of those genera; the results remain the same as in Aktipis et al. (2011). By extending taxon sampling, we further recovered within Hemitominae five other genera that had been previously assigned to Emarginulinae: *Profundisepta* McLean & Geiger, 1998, *Cornisepta* McLean & Geiger, 1998, *Zeidora* A. Adams, 1860, *Montfortista* Iredale, 1929 and *Hemimarginula* McLean, 2011 (Fig. 2). The name of the subfamily therefore becomes Zeidorinae Naef, 1911, with Hemitominae as a synonym. The subfamily Zeidorinae can be divided in three main clades: one containing the deep-sea genera *Cornisepta* and *Profundisepta*; one with *Zeidora*, *Hemitoma*, *Montfortista* and *Hemimarginula* (from here on referred to as *Hemitoma*-clade); and finally, a clade where *Cranopsis* is not monophyletic and appears nested within two clades of *Puncturella*.

Interestingly, *Rimula* Defrance, 1827, so far considered an Emarginulinae and here sampled with three species, was recovered with high posterior probability as the first splitting branch in the Fissurellidae tree, outside of any of the currently recognized subfamilies (Fig. 2). Although support for this placement was lower in the ML analysis (Supplementary Material), both methods reject its traditional position close to other genera in Emarginulinae.

Among the lineages of Emarginulinae, a large monophyletic group

containing a subclade of *Montfortula* Iredale, 1915 and *Variegemarginula* McLean, 2011 (both assigned to Hemitominae by McLean (2011) and neither monophyletic in our analyses) was recovered with high support as the sister group to a subclade including *Tugali* Gray, 1843 and *Scutus* Montfort, 1810, with both latter genera being monophyletic (Fig. 2). The diverse genus *Emarginula* was not monophyletic, being part of two lineages, one of which includes *Scelidotoma gigas* (Martens, 1881) among *Emarginula*.

Both Fissurellinae and Diodorinae were monophyletic and sister groups. Two clades were found in Fissurellinae, one composed exclusively of *Fissurella* Bruguière, 1789, and a second including *Fissurella* plus several additional genera: *Lucapinella* Pilsbry, 1890 (until now classified as Emarginulinae), *Macroschisma* Gray, 1835 and *Amblychilepas* Pilsbry, 1890 (neither of which were monophyletic), *Dendrofissurella* McLean & Kilburn, 1986 and *Medusafissurella* McLean & Kilburn, 1986, both monophyletic. In Diodorinae, early divergences separated *Cosmetalepas* Iredale, 1924, *Monodilepas* Finlay, 1926, *Fissurellidea* d'Orbigny, 1841 (until now classified as Emarginulinae) and *Megathura* Pilsbry, 1890 from a large clade of *Lucapina* G. B. Sowerby I, 1835 (monophyletic) and *Diodora* Gray, 1821 (not monophyletic).

The ML analysis of the same dataset resulted in a congruent topology, although the bootstrap support for many of the early splits was low, including support for the family node (Fig. 3). To explore the differences in the support of basal nodes, we created three additional ML datasets testing for the influence of saturated sites, poorly aligned regions and taxa with long branches. In the first subset, we eliminated the most saturated 3rd position of COI codons, which resulted in increased support for subclades of Zeidorinae (Fig. 3). In the second subset, we removed poorly aligned regions of ribosomal gene alignments with Gblocks (Talavera and Castresana, 2007), which had a smaller but similar effect (Fig. 3). In the third subset, we removed the *Hemitoma*-clade, which had a long branch; this had a major impact on the bootstrap support, increasing it to high values at the family node and Zeidorinae nodes (Fig. 3), in agreement with the BI. The support at the remaining basal nodes, be it low or high, was not affected by any of the three factors (Fig. 3); *Rimula* remained as the sister group to all

other fissurellids and Emarginulinae was not monophyletic in either treatment.

Gene trees had expected low support overall, with low resolution at deep branches, particularly for the slow evolving nuclear genes. Topologies generally reflect the major relationships recovered from the concatenated dataset, with different exceptions in each gene (Supplementary Material).

3.2. Taxonomy

The recovered phylogeny leads to the following proposed taxonomic changes.

Rimulinae Anton, 1838 **stat. nov.**
Type genus. *Rimula* Defrance, 1827
Included genera. *Rimula* Defrance, 1827
Diagnosis. Shell with a narrow and elongate foramen at or near the center of the anterior surface, closed on both ends. No internal septum. Selenizone extending from the fissure to the apex, which is recurved towards the posterior of the shell. Anterior slope convex; posterior slope concave or straight. Outer surface delicately cancellated with numerous ribs and concentric threads. Shell ranging from a few millimeters to slightly over one centimeter.
Remarks. Monotypic subfamily. *Rimula* differs from *Puncturella*, a similar-looking genus in the subfamily Zeidorinae, in not having an internal septum and in the position of the foramen, which varies in *Puncturella* from the middle of the anterior surface to near or at the apex. For almost 200 years, the family name Rimulidae has been included in the synonymy of Fissurellidae or Emarginulidae.

Zeidorinae Naef, 1911 **stat. nov.**
Type genus. *Zeidora* A. Adams, 1860
Junior synonym. Hemitominae Kuroda, Habe & Oyama, 1971 **syn. nov.**
Remarks. The oldest available name for the clade including the genera *Zeidora* and *Hemitoma* is Zidoridae Naef, 1911 (based on *Zidora* P. Fischer, 1885, an unjustified emendation of *Zeidora*), until now treated as a synonym of Emarginulinae.

Puncturella R. T. Lowe, 1827
Type species. *Patella noachina* Linnaeus, 1771
Junior synonyms. *Cemoria* Risso, 1826
Cranopsis A. Adams, 1860 **syn. nov.**
Sipho T. Brown, 1827

Emarginulinae Children, 1834
Montfortula Iredale, 1915
Type species. *Emarginula rugosa* Quoy & Gaimard, 1834
Junior synonyms. *Plagiorhytis* P. Fischer, 1885
Variegemarginula McLean, 2011 **syn. nov.**

The following genera are transferred between subfamilies: *Cornisepta*, *Profundisepta* and *Zeidora* from Emarginulinae to Zeidorinae; *Montfortula* from Zeidorinae to Emarginulinae; *Lucapinella* from Emarginulinae to Fissurellinae; *Fissurellidea* from Emarginulinae to Diodorinae.

3.3. Divergence dates

In contrast with the topology results presented in Section 3.1, Emarginulinae was recovered as monophyletic in the FBD dating analyses, but with low support (PP = 0.77 and 0.90 in the Triassic and Carboniferous analyses, respectively; Fig. 4). The topology in the ND chronograms was the same as in non-calibrated trees, with a non-monophyletic Emarginulinae and low support for relationships among its subclades (Supplementary Material).

Divergence time estimates from FBD analyses indicate that crown

Fissurellidae originated in the Jurassic around 175 Ma [95% highest posterior density intervals (HPD): 138–220 Ma (Triassic-FBD), 137–213 Ma (Carboniferous-FBD)] (Figs. 4 and 5). Including the fossil from the Carboniferous, which is about 75 million years older than the most accepted fissurellid fossil from the Triassic, did not result in contrasting inferences (Fig. 5, Supplementary Material). In ND analyses, calibrated nodes showed narrow intervals and reflected the age of the fossil used for calibration, as expected (Fig. 5). The age of the family, for example, was inferred to be close to the age of the oldest fossil in each analysis: 242 Ma [95% HPD: 238–246 Ma] (Triassic-ND), 313 Ma [95% HPD: 310–317 Ma] (Carboniferous-ND). A major difference between these two dating methods is that the FBD model allows the placement of fossils as stem lineages, therefore permitting crown groups to be younger than in ND approaches (example FBD trees with fossil tips are in the Supplementary Material).

For more recent nodes, both FBD and ND analyses inferred congruent origination times (Fig. 5), as noted for Diodorinae at ca. 77 Ma [95% HPD: 59–97 Ma (Triassic-FBD), 58–99 Ma (Carboniferous-FBD), 73–81 Ma (Triassic-ND, Carboniferous-ND)], for Fissurellinae at ca. 65 Ma [95% HPD: 43–82 Ma (Triassic-FBD), 37–78 Ma (Carboniferous-FBD), 50–87 Ma (Triassic-ND), 57–94 (Carboniferous-ND)], for their common ancestor at ca. 90 Ma [95% HPD: 73–109 Ma (Triassic-FBD), 70–110 Ma (Carboniferous-FBD), 78–113 Ma (Triassic-ND), 79–118 Ma (Carboniferous-ND)], and for Rimulinae at ca. 72 Ma [95% HPD: 39–109 Ma (Triassic-FBD), 27–103 Ma (Carboniferous-FBD), 73–81 Ma (Triassic-ND, Carboniferous-ND)].

3.4. Biogeographic history

Ancestral range reconstruction from BioGeoBEARS on the Triassic-FBD chronogram estimated DEC + j as the best model (Table 4), with inferred ancestral ranges being similar across all dated trees and most models (Supplementary Material). The family Fissurellidae was estimated to have originated in what today constitutes the Indo-West Pacific—the Tethys Sea of ca. 175 Ma (Fig. 6). For several million years they continued to diversify in that region forming the lineages leading to the modern Rimulinae, Zeidorinae and emarginuline genera.

With the opening of new oceans, fissurellids dispersed and diversified, forming the subfamilies Fissurellinae and Diodorinae around 60–90 Ma (Fig. 6). One of the major subclades of Fissurellinae retained an Indo-West Pacific distribution from where it dispersed to Southern Africa. The other subclade colonized the Western Atlantic and Eastern Pacific. A transatlantic dispersal then happened with the colonization of the west coast of Africa (Fig. 6). Diodorinae also had an early dispersal from the Indo-West Pacific to the Western Atlantic, where it diversified with *Lucapina* and *Diodora*. At the same time, a small early clade of Atlantic Diodorinae colonized the Eastern Pacific. Finally, a subclade of *Diodora* then crossed back eastward around 40 Ma, leaving lineages in the current Mediterranean Sea, and recolonizing Southern Africa and the Indo-West Pacific.

Fissurellinae and Diodorinae were not the only clades to disperse to the Atlantic, with some events leading other fissurellids (e.g., *Hemitoma*, *Zeidora, Rimula*) to the Western Atlantic (Fig. 6). The few Antarctic samples represented here originated recently from an Indo-West Pacific lineage of *Puncturella* (Fig. 6).

With few exceptions related to doubtful fossil identifications (see discussion below), the overall distribution of fissurellid fossil occurrences from the paleobiology database matches closely the ancestral areas estimated on the tree (Fig. 6A–F).

4. Discussion

4.1. Phylogenetic relationships and evolution of the shell

The extensive rearrangements observed for the position of genera traditionally considered Emarginulinae bring to light the fact that a
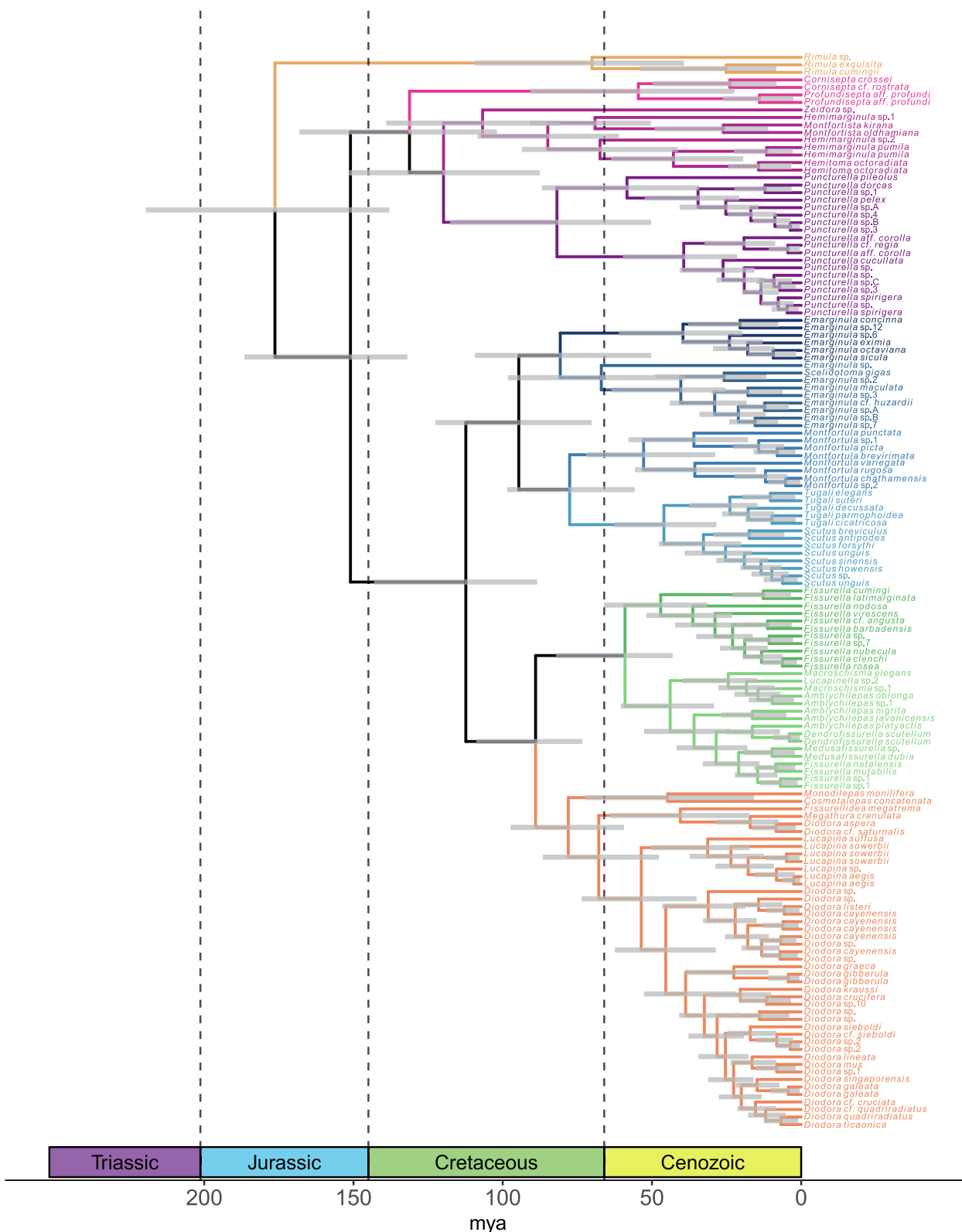
Fig. 4. Chronogram of Fissurellidae based on a fossilized birth-death analysis with 50 fossils, the oldest being from the Triassic period (Triassic-FBD). Horizontal bars on the nodes indicate the 95% highest posterior density intervals for divergence time estimates.

huge diversity of fissurellids has been historically grouped together on the basis of characters that are plesiomorphic for the family. Morphological classifications where Emarginulinae encompassed most fissurellid genera except the ones in Fissurellinae (McLean, 1984; Thiele, 1929) were supported by radular and sperm morphology:

Emarginulinae have a middle rachidian tooth of varying width, a large bicuspid outer lateral tooth, and sperm nucleus with a large anterior invagination housing an axial rod; Fissurellinae on the other hand have a narrow rachidian tooth with a tapered tip, a broad outer lateral tooth with three or four cusps, and sperm nucleus lacking the axial rod and
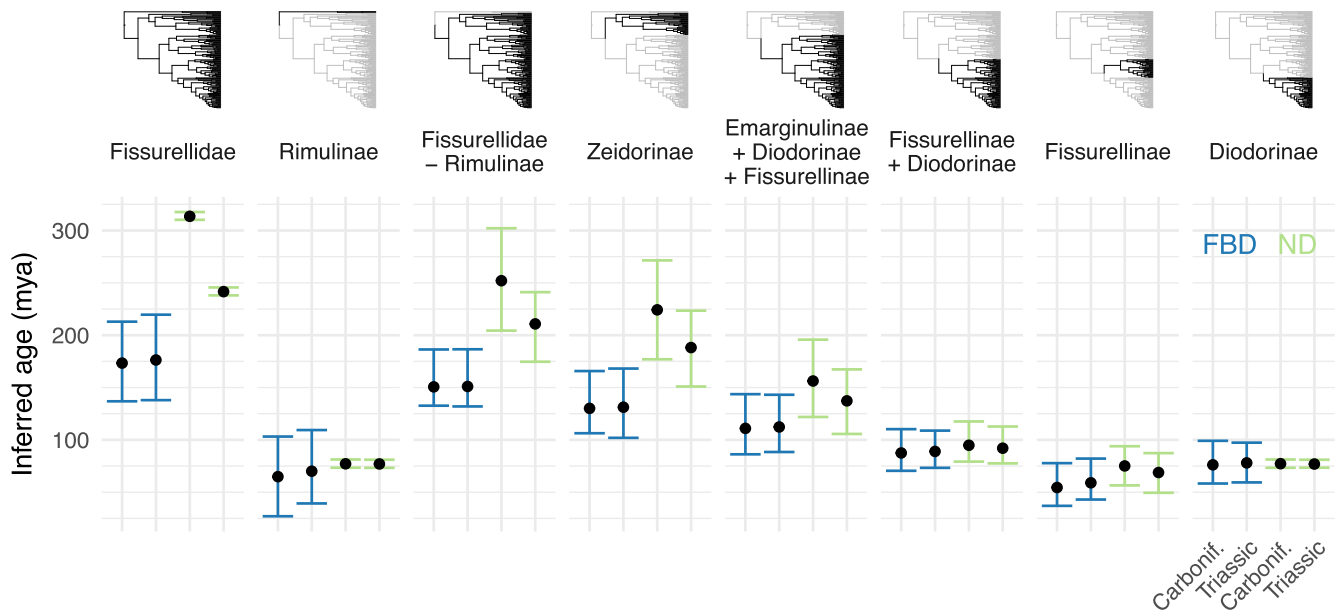
Fig. 5. Node age comparison among Bayesian dating analyses for basal nodes. Black circles represent median ages; error bars indicate 95% highest posterior density intervals for divergence time estimates. Fossilized birth-death (FBD, blue); node dating (ND, green). Triassic: *Emarginula muensteri* from the Triassic as the earliest fossil; Carboniferous: *Retshitsella egorovi* from the Carboniferous added as the earliest fossil.

invagination (Hodgson and Foster, 1992; McLean, 1984; Thiele, 1929). The phylogeny presented here indicates that the emarginuline structure of the radula and sperm are therefore ancestral states for the family. Members of Diodorinae were later distinguished from Emarginulinae on the basis of soft anatomy, lacking the axial rod in the sperm nucleus (Hodgson and Chia, 1993) and the hook-shaped process of the shell muscle present in other Emarginulinae (McLean, 1984), while diverging from Fissurellinae based on the presence of a depression on the posterior part of the callus, the internal ring surrounding the shell foramen (McLean, 1984).

With a molecular phylogeny, Aktipis et al. (2011) reinstated the subfamily Hemitominae (now Zeidorinae) containing three genera that were then considered part of Emarginulinae: *Hemitoma*, *Puncturella* and *Cranopsis*. We confirm the position of these three genera in Zeidorinae and further recover five other genera in this subfamily: *Profundisepta*, *Cornisepta*, *Zeidora*, *Hemimarginula* and *Montfortista* (Fig. 2). Contrary to the proposition of McLean (2011), it is clear that Zeidorinae does not contain only taxa with a short slit or notch, but also includes species with a foramen on the anterior surface of the shell (*Puncturella*; Fig. 2C), a pronounced marginal slit (*Zeidora*) or a subapical/apical foramen (*Profundisepta*, *Cornisepta*). Based on the reduction of the shell slit and on one radular character, McLean (2011) included nine genera in Hemitominae. With the molecular phylogeny, we provide evidence to retain *Hemitoma*, *Hemimarginula* and *Montfortista* in Zeidorinae. Nonetheless, not only we find other genera as part of Zeidorinae, but we also find that *Variegemarginula* and *Montfortula*, assigned to Hemitominae by

McLean (2011), actually form a clade within the Emarginulinae grade in our phylogeny (Fig. 2). Both genera present short slits, visible either dorsally or mostly in anterior view (Fig. 2E), and their sister group is a clade of *Scutus* and *Tugali*, genera lacking or with only a weak anterior depression on the shell (Fig. 2F), revealing this to be a large clade with reduction of the slit. Species of *Variegemarginula* were found nested within *Montfortula*, and the former is here synonymized with *Montfortula*. They differ from McLean's hemitomine genera *Hemimarginula* and *Octomarginula*, which also have short slits, but more heterogeneous ribs – usually three broader ribs making a raised anterior slope in *Hemimarginula* (Fig. 2B), and eight strong primary ribs in *Octomarginula*, while *Montfortula* has fine radial ribs almost uniform in size or alternating between primary and secondary ribs (Fig. 2E) (McLean, 2011). We therefore recognize the reduction of the shell fissure as something that happened at least three times in fissurellids: once in a subclade of Zeidorinae, in the lineage leading to *Hemitoma*, *Hemimarginula* and *Montfortista*; another in a clade of *Montfortula*, *Scutus* and *Tugali*; and a third time in *Scelidotoma* McLean, 1966 (see below). A denser morphological analysis throughout the family is needed to clarify the distribution of radular states. McLean (2011) himself notes a striking similarity between the radula of *Profundisepta* with that of his Hemitominae (Zeidorinae), which is in agreement with our placement of *Profundisepta* in this subfamily.

The genus *Rimula*, sampled here with three species, was recovered as the sister group to all other fissurellids. This topology had been found once before in a vetigastropod study with a combined analysis of two

Table 4
Model test results from BioGeoBEARS based on the Triassic-FBD calibrated tree, ordered by AICc weights. The best fitting model is highlighted in bold. LnL, log-likelihoods; params, number of parameters in the model; *d*, dispersal rates; *e*, extinction rates; *j*, jump dispersal rates; AICc, sample size corrected Akaike Information Criterion scores; AICc_wt, Akaike weights.

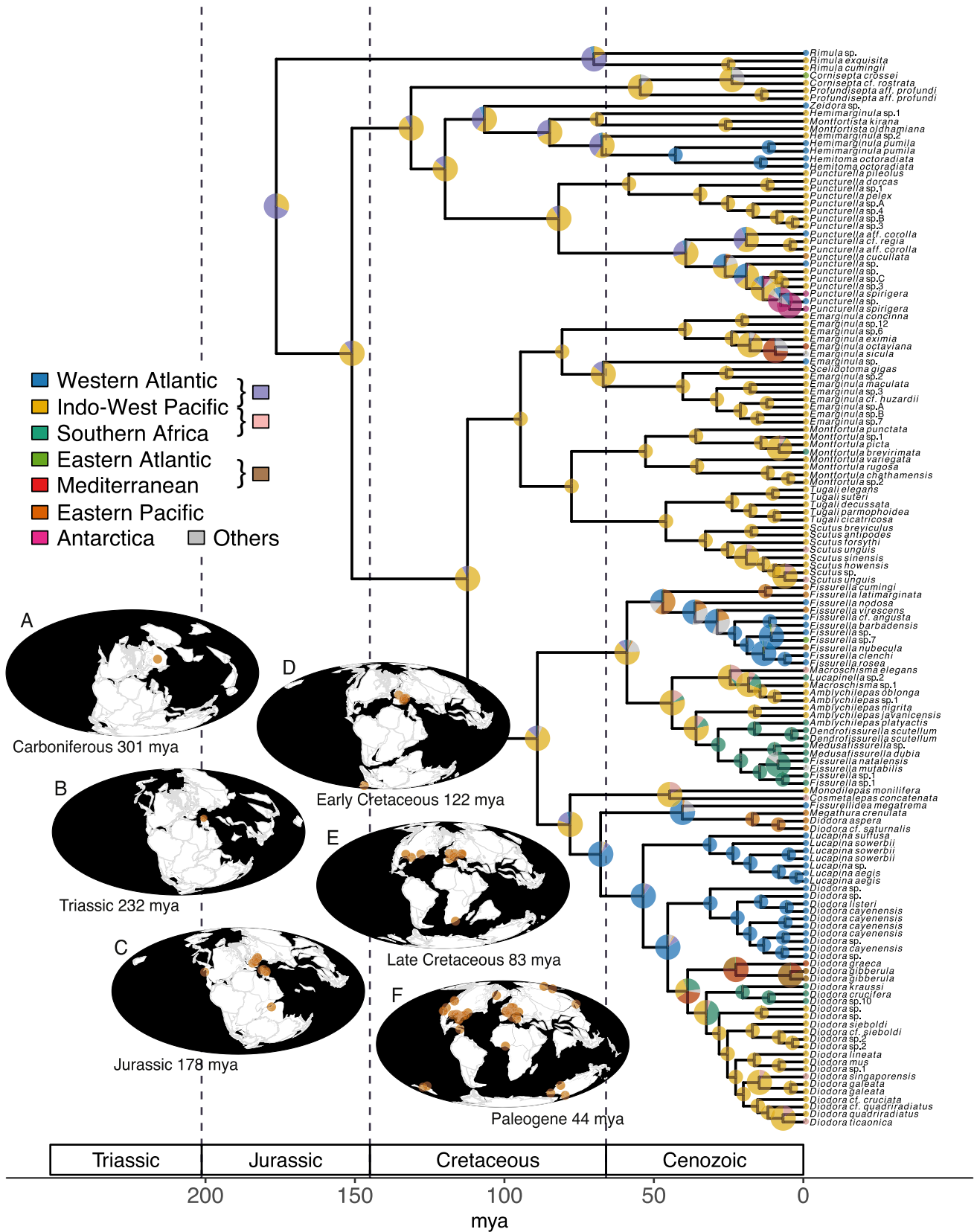|	LnL	params	*d*	*e*	*j*	AICc	AICc_wt
DECj	**−188.1**	**3**	**0.0005**	**1.00E−12**	**0.014**	**382.4**	**0.68**
BAYAREALIKEj	−189	3	0.0003	1.00E−12	0.017	384.2	0.28
DIVALIKEj	−190.9	3	0.0006	1.00E−12	0.013	387.9	0.043
DIVALIKE	−202.9	2	0.0012	9.70E−05	0	409.9	7.20E−07
DEC	−207.4	2	0.0011	5.00E−05	0	418.9	8.10E−09
BAYAREALIKE	−244.6	2	0.0013	0.0072	0	493.2	5.90E−25

Fig. 6. Ancestral range reconstruction on the Triassic-FBD calibrated tree of fissurellids with the best fitting DEC + *j* model in BioGeoBEARS. Pie charts are smaller on nodes in which the state probability of one area is equal or larger than 95%. Biogeographical regions: Western Atlantic, Eastern Atlantic, Mediterranean, Southern Africa, Indo-West Pacific, Eastern Pacific, Antarctica; brackets indicate wider ancestral ranges that combine the specified basins; ancestral areas with small probabilities were combined into Others. Paleomaps modified from the Paleobiology Database Navigator (https://paleobiodb.org/navigator): continent configuration at the time indicated in each map; circles represent all fissurellid fossil occurrences in the named geological period.

genes and six fissurellid terminals (Kano, 2008). The position of *Rimula* outside of the currently recognized subfamilies warrants its recognition as a subfamily, for which the name Rimulinae Anton, 1838 status nov. is available. *Rimula* has a foramen in the center of the anterior surface of the shell (Fig. 2A). The following split in the tree is between Zeidorinae (with varying conditions of the foramen; Fig. 2B–C) and the remaining fissurellids (Emarginulinae with marginal slits/notches plus Fissurellinae and Diodorinae with an apical foramen; Fig. 2D–J). The position and shape of the foramen therefore is homoplastic and has a more complex history than the direct progression from marginal to apical, as proposed from morphological analyses and an older classification (McLean and Geiger, 1998). At least two independent origins in different subfamilies can be traced for a deep marginal slit (*Zeidora*, *Emarginula*), for an apical foramen (*Cornisepta*, Diodorinae and Fissurellinae), and for the reduction of the fissure (*Hemitoma*, *Scutus* and their related genera) (Fig. 2). Given the mid-surface placement of the foramen in *Rimula* and some zeidorine, this could represent the ancestral condition for the family, although the inclusion of further unsampled genera of the traditional Emarginulinae will be key for a more accurate state reconstruction.

Another conspicuous shell feature present in some fissurellids is a septum that partially divides the interior of the shell extending from near the apex (Farfante, 1947). Following the progressive evolution of traits from the morphological analyses of McLean and Geiger (1998), the absence of a septum in *Emarginula* was considered the plesiomorphic condition, with a well-developed septum in forms like *Puncturella*, which was then inferred to be reduced to a truncated callus in *Diodora*. Our molecular results agree that the ancestral fissurellid likely lacked a septum (absent in Rimulinae, Emarginulinae, Diodorinae and Fissurellinae). The placement of the septate *Puncturella*, *Zeidora*, *Cornisepta* and *Profundisepta* all in Zeidorinae indicates that this is likely a new condition originating in this subfamily, perhaps associated with deep sea taxa, given its absence in the intertidal and shallow-water *Hemitoma*, *Hemimarginula* and *Montfortista*. It also suggests that the truncated callus of Diodorinae is not homologous with the septum.

Many of the most diverse and stereotypical fissurellid genera are currently not monophyletic. *Emarginula* consists of at least two independent lineages (Fig. 2). Nonetheless, we withhold from making any taxonomic changes until the type species *E. fissura* (Linnaeus, 1758) is included in a phylogeny to determine which clade will retain the genus name. *Scelidotoma* was recovered within one of the clades of *Emarginula*. Its position is distant to *Tugali*, consistent with McLean's (1966) description of *Scelidotoma* as a new genus, and indicates yet another event of reduction of the shell fissure.

The few specimens that were identified as species of *Cranopsis* are nested among the many sampled *Puncturella*. In general, unless an individual can be specifically identified as a described species, distinction between the two genera is difficult. *Cranopsis* was treated as a subgenus of *Puncturella* in the past. The two genera have been diagnosed on the basis of the relative position of the foramen (mid position of anterior surface on *Cranopsis*; closer to the apex in *Puncturella*; Fig. 2C) (Farfante, 1947), and degree of development of the internal septum (more so in *Puncturella*) (Herbert and Kilburn, 1986). These however are not discrete features easily separable. The presence of a double rib anterior to the foramen of *Cranopsis* has also been used as a distinguishing character, which is associated to an internal seam in the shell and with a split in the mantle skirt anterior to the foramen (McLean and Geiger, 1998). Nonetheless, the presence of an internal seam and a double rib seem to be variable and more or less pronounced depending on the species (Herbert and Kilburn, 1986). Due to the phylogenetic position of the sampled species, together with the ambiguous definitions of the two genera, we synonymize *Cranopsis* with *Puncturella*. There are two well delimited clades of *Puncturella*, and detailed observation of the shells and mantle in the future could reveal new traits that are associated to these natural groups.

Fissurella is another non-monophyletic genus, present in the two

subclades of Fissurellinae, only one of which includes other genera (Fig. 2). The inclusion of the type species *F. nimbosa* (Linnaeus, 1758) is necessary to determine which clade retains the genus name. Fissurellinae presents great geographical structure between the two subclades, one being present in the Atlantic and Eastern Pacific, while the other is in Southern Africa and the Indo-West Pacific. *Fissurella nimbosa* is restricted to the Western Atlantic, indicating a likely position in the Atlantic clade. A reassessment of other Fissurellinae genera is also necessary, given the non-monophyletic status of *Amblychilepas* and *Macroschisma*.

Among Diodorinae, *Lucapina* is monophyletic and the sister group to a large clade of *Diodora* (Fig. 2), including *D. graeca* (Linnaeus, 1758), the type species of the genus. This is a very diverse clade of *Diodora*, present in most modern oceans and diverged ca. 45 Ma. However, a smaller clade of *Diodora* from the Eastern Pacific (where no *Diodora* from the larger clade is present) was also recovered as the sister group to *Megathura crenulata* (Sowerby I, 1825), the only species in the genus and found in the same area. The Eastern Pacific species of *Diodora*, *D. aspera* (Rathke, 1833) and *D.* cf. *saturnalis*, therefore, require a new generic allocation.

Finally, *Hemimarginula* was paraphyletic, including species of *Hemitoma* and *Montfortista*. Since it is nested in a clade with overall reduction of the foramen, it is possible that the short slit of *Hemimarginula* (Fig. 2B) was plesiomorphic in that clade, and that the condition was retained in several non-sister species. McLean (2011) characterized *Hemimarginula* by having a short slit and three primary ribs that raise the anterior surface of the shell in a triangular shape. Although these traits are clear in some of our specimens and sufficient to allow identification in the genus, *H. pumila* has less pronounced anterior ribs and is more similar to *Hemitoma* in shape, consistent with their sister relationship in our phylogeny. Further sampling in this group and study of the *Hemimarginula*-shaped shell is necessary to clarify the classification of these species.

4.2. Time of origin and oceanic dispersal

Two calibration methods – node dating (ND) and fossilized birth–death (FBD) – and two different oldest fossil – from the Triassic and Carboniferous – were used in combination for a total of four divergence time analyses. Our FBD trees estimate a younger age than previously hypothesized for Fissurellidae, indicating an origin in the Jurassic around 175 Ma, with the highest posterior density intervals between late Triassic to early Cretaceous (Figs. 4 and 5). No significant difference was found with the inclusion of the Carboniferous fossil. Estimates from ND analyses were older, inferring family ages close to the fossil ages used as constrains. The two methods mostly differed because the FBD model allows fossils to be placed as stem lineages, permitting younger ages for crown groups, a scenario that is impossible for ND analyses to recover given the node calibrations that need to be assigned. Similar results have been recovered in calibration comparisons for other animal groups (Kim et al., 2018). Due to the FBD model being better at handling the available fossil information, it was our preferred analysis to carry out the biogeographic reconstruction. One other study has calibrated a fissurellid tree, but focusing on endemic species of the Cape Verde archipelago (R.L. Cunha et al., 2017). The inclusion of only one fossil and one geographical calibration, together with the limited sampling of species out of the target locality, led to severely underestimated ages across the tree (e.g., estimated family age of ca. 44 Ma), in strong disagreement with the fossil record.

Ancestral range reconstruction showed strong geographical structure in the distribution of fissurellids (Fig. 6), in agreement with our hypothesis based on the short-lived, non-feeding larvae of the group (Giese and Pearse, 1977; Hadfield et al., 1997; Lewis, 1960; Reynoso-Granados et al., 2007) and on previous data on the genetic structure of populations at small geographical scales (R.L. Cunha et al., 2017; Waters et al., 2007). In their long evolutionary history of about 175

million years, few events of long-range dispersal are observed in the tree (Fig. 6). Given the biogeographical pattern and larval biology of these keyhole and slit limpets, either slow migration across coastlines and/or rare events of dispersal are responsible for the transoceanic movements and large-scale diversification processes of fissurellids. Comparable with our results, other gastropod groups with wide distributions (e.g., whelks and true limpets) also show capacity of reaching distant locations while keeping marked geographical structure, suggesting that even for benthic organisms with short-lived larvae or intracapsular development, dispersal at long evolutionary timescales is possible (Donald et al., 2015; Nakano and Ozawa, 2004; Vaux et al., 2017), as has also been shown for low vagility terrestrial taxa such as harvestmen (Sharma and Giribet, 2012). Founder speciation in the marine environment (even for poor dispersers) could be more common than previously recognized (Kirkendale and Meyer, 2004; Paulay and Meyer, 2002).

Fossil evidence supports the biogeographical reconstruction inferred here. The oldest occurrences of fissurellids (considering either the Triassic or the Carboniferous; Fig. 6A,B) are from modern landmasses that were once bordering the Tethys Sea. It is not until Laurasia and Gondwana start to separate, and a connection between the Tethys and the forming Atlantic Ocean is established, that fissurellid fossils are seen on the coasts of the Americas (Fig. 6D,E). The age of such fossils supports the hypothesis that dispersal happened westward through the Tethys Seaway, and not by crossing the large Panthalassa *curr.* Pacific Ocean. One record from the Upper Jurassic (ca. 150 Ma; Fig. 6C) from the Eastern Pacific (Kiel et al., 2008) could contradict this account; nonetheless, the study is a description of other groups of gastropods from California, where only one individual fossil identified as *Fissurella?* is cited, with no description or image. Given that the fossil is ca. 85 million years apart from our estimated age for Fissurellinae and that no data about the specimen are available in the paper, we find that this is likely a misidentification and possibly not even a fissurellid. From the fossils that we included in our dating analyses based on proper identification, all but one were collected in localities that match the model-estimated distribution of the clade at the time the individual was living (Table 3). The only exception is PaleoDB collection 7791, a [Diodorinae, Fissurellinae] from ca. 60 Ma from Nigeria. It is older than the first appearance of an Eastern Atlantic clade in our reconstruction, but not older than the origin of Western Atlantic [Diodorinae, Fissurellinae]. This indicates that the lineage of this fossil might not have left living descendants, or that we have not sampled them in the molecular phylogeny. Finally, fossils from the modern Mediterranean region show that some lineages that today are restricted to the Indo-West Pacific (e.g., *Montfortula*) were once more widespread (Table 3), indicating that the Indo-West Pacific has had an important role in both the origin of new lineages and maintenance of old ones, as also observed for other vetigastropods (Williams, 2007).

Although the Eastern Pacific Barrier has always been recognized as an important obstacle to transoceanic dispersal, genetic connections between transpacific species of sea urchins have been found (Lessios et al., 1998). According to our biogeographical reconstruction, in the millions of years of fissurellid evolution prior to the breakup of Pangea, not once do we observe a transition from the Tethys Sea *curr.* Indo-West Pacific to the Eastern Pacific (Fig. 6), suggesting that, at least for fissurellids and for other animals with similar short-lived larvae such as patellogastropods (Nakano and Ozawa, 2004), the Panthalassa *curr.* Pacific Ocean indeed was too large of a barrier for dispersal. Upon the opening of an oceanic connection between Africa and Europe, major transitions by different lineages of fissurellids led to the colonization of new oceans (Atlantic, Mediterranean), as well as of the Eastern Pacific via the Central American Seaway, as exemplified by the Diodorinae. Further evidence comes from the fact that since the closure of the Tethys Seaway in the early Miocene, few transoceanic events took place, and those are restricted to dispersals between the Western Indian and Indo-West Pacific oceans, across the Atlantic and to Antarctic waters,

but not across the Pacific (Fig. 6).

In the only other model-based biogeographical study of a globally distributed mollusk family, Herrera et al. (2015) also found that cardiid bivalves from the Indo-West Pacific dispersed westward via the Tethys Seaway. However, these clams went on to colonize the Eastern Atlantic, while Western Atlantic clades seem to have originated from Pacific ancestors, functioning only as a recipient of diversity and not as a source of new clades. This contrasts with our reconstructed biogeographical history of fissurellids, where Western Atlantic clades were an important source of diversity to the colonization of the Eastern Atlantic, the Eastern Pacific, and to a large recolonization of Southern Africa and the Indo-West Pacific via the Tethys Seaway *curr.* Mediterranean Sea (Fig. 6).

The oldest existing seafloors are from the eastern Mediterranean Sea (Granot, 2016), and there are many fissurellid fossils from modern European territories from the Mesozoic, however, no current fissurellid lineage from the Mediterranean has ancestors older than about 20 million years in the same basin (Fig. 6). These observations seem to confirm that the modern Mediterranean fauna is the outcome of relatively recent colonization events, and that past local faunas that participated in the early transitions from the Tethys to the Atlantic have completely gone extinct. The time of origin of Mediterranean lineages could also provide insights about the consequences of the Messinian Salinity Crisis ca. 5.6 Ma to local biodiversity. A recent history of divergences in the Mediterranean would suggest that fissurellids survived the crisis in the late Miocene, and therefore that the drying out of the basin was perhaps incomplete, as inferred by some other studies (Carnevale et al., 2008, 2006; Meijer and Krijgsman, 2005). However, because most of the Mediterranean species sampled here have wider distributions, it is possible that species surviving in the nearby Eastern Atlantic then dispersed to the Mediterranean after the refilling of the basin. Future sampling of more Mediterranean endemics will be a key source of biological evidence in this debate.

5. Conclusions

We present the largest phylogeny of fissurellids to date and provide one of the most comprehensive and integrative datasets to study the evolution and biogeography of marine invertebrate taxa by combining molecular, geographical and fossil data. We highlight the need for major taxonomic revisions, especially of the most diverse genera e.g., *Emarginula*, *Fissurella*, *Diodora*. Our inferred topology shows that many genera previously placed in Emarginulinae are recovered in other subfamilies and other genera may further form a grade deep in the tree, indicating that the traditional Emarginulinae had been defined by plesiomorphic conditions. However, relationships between subclades of Emarginulinae and the [Fissurellinae, Diodorinae] clade are yet to be resolved, and likely require additional genomic data.

The recovered topology reveals a complex history for the evolution of the shell foramen, with independent origins for the apical foramen and for the reduced or closed slit. The marginal slit, often considered the plesiomorphic condition, could be derived from a foramen on the anterior surface of the shell. We recommend that future molecular and morphological studies prioritize and expand sampling of genera still placed in the traditional Emarginulinae, from which we could gain the most insights about the ancestral traits and early transitions in the evolution of the Fissurellidae.

Although fissurellid fossils are abundant, many can only be assigned to subfamilies due to the lack of defining features in the shells, coupled with the non-monophyletic condition of many genera. A more extensive and comparative assessment of the morphology of the shell, including microstructure and detailed data on the shell surface, is necessary to improve the use of the available fossil record and to find potential synapomorphies of specific clades.

Biogeographical reconstructions based on calibrated trees and supported by fossil information indicate that crown fissurellids originated

ca. 175 Ma in the Tethys Sea *curr.* Indo-West Pacific. The tropical seaway connecting the Tethys to the Atlantic upon the breakup of Pangea was an important passage for the westward dispersal of fissurellids. As seen for many marine taxa, the Indo-West Pacific is house to a large diversity of fissurellids, functioning both as a place of origin, but also of maintenance of diversity that might have gone extinct elsewhere. Fissurellids had a long time to diversify in the Indo-West Pacific, but they were also successful in colonizing and diversifying in the Western Atlantic, which served as a source for further dispersal and diversification in many other oceanic regions. The larval biology and limited dispersal capacity of fissurellids produce a structured geographic distribution in the phylogeny, but dispersal through long evolutionary time allowed them to reach a worldwide distribution. The variety of patterns of genetic structure and dispersal routes inferred for these and other marine invertebrates reflect the complex set of factors driving evolution in the marine environment. Expanding the use of integrative data on marine invertebrate taxa is key to furthering our understanding about evolution in the sea, as exemplified here with fissurellids.

Author contributions

TJC and GG conceived and designed the study. TJC, PB, YK and GG collected and identified specimens. TJC, SL and YK carried out molecular lab work. TJC collected fossil information, analyzed the data and drafted the manuscript. All authors contributed to the manuscript and gave final approval for publication.

Appendix A. Supplementary material

Supplementary data to this article can be found online in Harvard Dataverse at https://doi.org/10.7910/DVN/CJSSLM.

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